T H E S I S

THE BIOLOGICAL CONTROL OF THE FALL WEBWORM IN COLORADO

Submitted by

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In partial fulfillment of the requirements
for the Degree of Master of Science
Colorado State College
Fort Collins, Colorado

June 1936

ACKNOWLEDGMENT

The writer is indebted to Dr. C. R. Jones of the Department of Entomology and Zoology of the Colorado State College, for making this study possible, and to each member of the staff of that department for many helpful suggestions. If the observations upon the webworm parasites have any value, it is due in large measure to the determinations of species by Mr. C. F. W. Muesebeck, Mr. A. B. Gahan, and Mr. R. A. Cushman of the United States National Museum, and by Dr. H. J. Reinhard of the Texas Agricultural Experiment Station. This is but a partial list of the many gentlemen to whom he is obligated for information bearing upon the webworm problem or for study material.

COLORADO STATE COLLEGE

OF

AGRICULTURE AND MECHANIC ARTS

April 20, 1936

I HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER MY SUPERVISION BY Ralph B. Swain

ENTITLED The Biological Control of the Fall Webworm in Colorado.

BE ACCEPTED AS FULFILLING THIS PART OF THE REQUIREMENTS FOR THE DEGREE OF MASTER OF Science

MAJORING IN Entomology

CREDITS 10

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INTRODUCTION

This study is concerned with the biological control of the fall webworm, Hyphantria cunea Drury, particularly in the State of Colorado, and the relationships of the webworm parasites and predators to their host and to each other.

When beginning work on this problem in the fall of 1934, the writer was told that the webworm occurred in the eastern plains region of the state, frequently in outbreak proportions, but that it was almost always present in goodly numbers in the canons of the eastern foothills at elevations of from five thousand to perhaps seven thousand five hundred feet. In the fall of 1934 many narrow-leaved cottonwoods in the cano mmouths a few miles west of Fort Collins were completely stripped of foliage by webworms. Webs were also numerous on the wild chokecherry, and higher up, on the alder. The writer was informed by Dr. George M. List, State Entomologist, that webs were conspicuous south of Fort Collins as far as Colorado Springs, and west from that point to Buena Vista. Since the defoliation of the trees mentioned was severe and widespread throughout the foothill region, 1934 might be called at least a mild outbreak year.

In 1935 the infestation over the same area was in the writer's judgement more severe. There were at least thirty to fifty percent more webs in the Buckhorn Canon than there were in 1934. Moreover, webs appeared in the city of Fort Collins and in nearby orchards where the previous year there had been none.

The area from which egg masses and larvae were collected and where field observations were mostly made is roughly a rectangular section of the foothills eight miles west of Fort Collins. It is about fifteen miles square and includes Spring, Buckhorn, Dixon, Rist, and Poudre Canons. The greatest infestation was usually near the mouths of the canons at an elevation of about five thousand feet, extending westward some twenty-five or thirty miles where the elevation might reach seven thousand to possibly seven thousand five hundred feet.

It will be seen that with the field of observation of the webworms narrowed down to a particular area and to supplementary insectary experiments, the problem of natural control factors was necessarily localized. Since diseases and predators played insignificant roles in the study area, the hymenopterous parasites, major control factors, received the most attention.

Female moth with egg mass on apple leaf.

(1½ times natural size.)

Photo by Grant Eddy.

Figure 1.

STATEMENT OF PROBLEM AND METHOD OF PROCEDURE

It has been repeatedly remarked that outbreaks of the fall webworm are apparently brought under control through the activities of a variety of insect parasites, predators, bird or insect, or through the ravages of disease. During the time between outbreaks the webworm population is believed to be held in check by any or all of these control factors.

The object of this study was to determine, if possible, what biological control factors were operating against the increase of the fall webworm in Colorado, and whether or not these factors were operating successfully.

At the outset it was believed necessary to ascertain the exact taxonomic status of the webworm, since the entomological literature of the last hundred years refers to at least two species of Hyphantria. A review of the literature was therefore undertaken, the opinions of eminent lepidopterists were sought, and comparisons of the genitalia of the local and eastern forms of the moths were made.

A thorough knowledge of the life history and behaviour of the host insect is necessary if parasite relationships are to be understood. For this reason the fall webworm was reared in the insectary from adult to adult, and weekly observations of the webworms in the field, from time of emergence to time of pupation, were made. It was believed that from the insectary studies and field observations an adequate understanding of the life history of <u>Hyphantria</u> could be gained.

Field observations were also relied upon to furnish information as to the relative importance of the various biological control factors. In order to place the determination upon a quantitative basis it was thought advisable to find by actual count, the average number of eggs laid by a single webworm moth, the average number of infertile eggs per egg mass, the average number of webworm larvae surviving the season and pupating in the fall, and the percentage of parasitism of each parasite.

Due to the possibility of alternate hosts for the major parasites, a general survey of the lepidopterous insects and their parasites in the study area was made. The webworm populations of the 1934 and 1935 seasons were roughly estimated so that the influence of control factors from one year to the next might be understood.

INVESTIGATION

A. TAXONOMIC STATUS OF THE FALL WEBWORM

The fall webworm, *Hyphantria cunea* Drury, is the only nearctic representative of a small genus of the *Arctiidae*. *H. penthetria* is described from Mexico, *H. postalbida* from Central Africa, *H. atripes* from the Gold Coast, West Africa, and *H. strigulosa* from Natal, South Africa.

The insect was first figured and described by D. Drury as *Bombyx cunea*, in his "Illustrations of Natural History, etc.," printed in London in 1770. Figure four of plate eighteen in that work is a reproduction of a spotted male collected in the vicinity of New York.

Since the original description has been carelessly quoted by some authors, it is here given as it appears in the original document.

"Plate 18, figure 4, Description on page 36.
Fig. iv. Expands an Inch and three-eighths.

Upper-side.--The Antennae, are pectinated and black. ---The Eyes the same. There is no appearance of any tongue.---The Head, is white.---The Back and Abdomen, ash colour.---The Superior Wings, are white; with a great number of spots differently shaped, of a faint black, or rather soot colour.---On the external edges, are five spots; those nearest the tips, being shaped like triangles.----The Inferior Wings, are white; with a sooty spot on each near the external edge, and a very faint small mark near the upper corner.

Under-side.--- The Legs, are black.--- The breast and Abdomen, ash colour.--- The same marks are to be seen here as on the upper side.

I received it from, New York.
I have not seen it described in any author."

The taxonomic status of the fall webworm has been the subject of much dispute since about the middle of the last century. Drury called the moth Bombyx cunea. Walker placed insects he believed to be the same species in the genus Spilosoma. Harris in "Insects Injurious to Vegetation", edited by Flint in 1862, described the webworm as it occurs in New England, giving it the name Arctia textor and further proposing the name Hyphantria for a possible new genus to include both his species and Arctia punctatissima Abbot and Smith, the webworm described from the South.

During the years 1899-1900 a series of papers appeared in the Canadian Entomologist all concerned with the Bombyx cunea controversy. Six entomologists participated, and a great deal of information was brought to light. However, the question was not settled to the satisfaction of all and is not to this day.

Studies of the genitalia have revealed no distinct difference between the webworms of various widely separated portions of the United States, or between the spotted and spotless forms. The writer can find no differences in the genitalia of the form studied at Fort Collins and the heavily spotted form occurring in Ohio. Mr. Foster H. Benjamin, of the United States National Museum, who has made a rather extensive study of the genitalia of the two supposed species, cunea and textor, states in a letter to the writer --"I suspect that all (referring to the several species and forms of the literature) are conspecific, and that at the very most, textor is an unstable and poorly defined upper austral-Canadian race of cunea." Other lepidopterists consider the webworm to be of two species. Dr. Wm. Forbes called the Fort Collins material a large phase of H. textor, although he admits the difficulty in distinguishing many forms of the moths and states that textor and cunea may possibly be conspecific. A portion of his letter describing Dyar's idea of the specific differences may be worth quoting, since in a few words it gives a picture of the two principal forms.

"e-- on the whole, cunea is southern, double-brooded, marked with black, at least in the male, and in the limiting case only on the shaft of the antenna, and the larva tends to be greenish tinted in its pale phase, and rather grayish brown in the dark phase. Textor is northern, single-brooded, never shows black marking, and the pale larva is light ash gray while the dark larva is a warm chocolate brown."

In reading the mass of literature on Hyphantria the writer finds statements to the effect that moths from white through all degrees of spottedness have been reared from a single female moth, and that pale yellowish-brown to black-headed larvae may occur in the same colony. Also, the webworm at Omaha, Nebraska, according to Bruner (53), may be double or single brooded according to the weather conditions, and it appears that the same situation is found in Connecticut, where in the southern portion of the state two broods may occasionallly be found, while the rule is a single brood.

Barnes and McDunnough in their "Check List of the Lepidoptera of Boreal America", 1917, give the following synonomy for Hyphantria:-

"Hyphantria Harris

958 textor Harr.

candida Wlk.

959 cunea Dru.

punctatissima A. & S.

budea Hbn.

punctata Fitch

pallida Pack.

suffusa Stkr.

brunnea Stkr.

959, 1 aspera Grt."

It would, under the circumstances, be absurd to treat the literature on the fall webworm as referring to several different species, because of the impossibility of determining to what form the writer refers. Since genitalic and structural differences have not been found, and marking, habits, and numbers of broods seem to signify nothing taxonomically, the fall webworm will here be treated as one species, Hyphantria cunea Drury.

B. THE LIFE HISTORY OF THE FALL WEBWORM IN COLORADO

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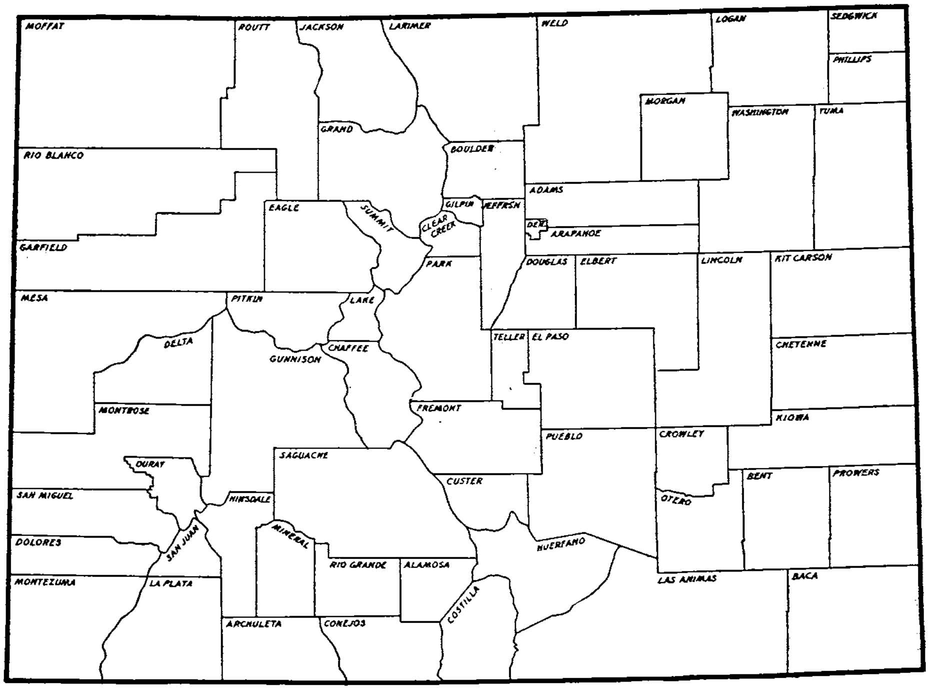
DISTRIBUTION AND CYCLIC OCCURRENCE

The fall webworm is generally distributed over the United States and Southern Canada. It has been a conspicuous pest of shade and orchard trees in the East and South of this country for many years. On the great plains, and in the higher mountains the webworm does not occur or is rare because of the absence of suitable host plants. It is present, often in damaging numbers, on the west coasts of both the United States and Canada.

In Colorado the webworm is most abundant in the eastern foothills of the Rocky Mountains. The area of infestation during the years 1934 and 1935 is roughly indicated on Map 1. The writer's observations are confined to but two seasons, but according to trustworthy report the population of webworms in the foothills has been large and fairly stable over a considerable period of years. A possible explanation for this situation will be brought out during the discussion of the parasite relationships.

A. B. Baird in a paper entitled, "An historical account of the forest tent caterpillar and of the fall webworm in North America", (11), 1916, summarized in an interesting manner all that had been recorded concerning outbreaks of the fall webworm. Stability of population has never been a characteristic of the webworm in the deciduous forest regions of North America. Serious outbreaks with defoliation of millions of valuable shade, forest, and orchard trees are definitely periodic. In the recorded cases, contol was effected by parasites, or less often, by disease.



Map 1.

The known area of webworm infestation, season of 1934.

HOST PLANTS

The fall webworm is a general feeder upon deciduous trees and shrubs. A complete list of the plants upon which it has been found would have little significance, and would be too long to include here. Riley, (377), lists one hundred and ten plants attacked by webworms during the Washington epidemic. Some slight preference in food plant is shown, the larvae being driven to some plants obviously because of a shortage of the favorite food. The nine plants Riley observed as receiving the most injury are listed below in the order of importance.

Balsam poplar *Populus balsamifera*
American aspen *Populus tremuloides*
White ash *Fraxinus americana*
European ash *Fraxinus excelsior*
Elder *Sambucus canadensis*
Cultivated pear and apple *Pyrus* spp.
Cherries *Prunus avium* and *cerasus*
Lilac *Syringa vulgaris*
Holly *Ilex* sp.

In the study area west of Fort Collins, three plants were distinctly the preferred host plants. These were the chokecherry, the narrow-leaved cottonwood, and the alder. However, the first two are the chief trees in the lower foothill region, and the last is one of the most abundant deciduous trees in the upper regions. A complete list of the plants upon which *Hyphantria* was found feeding follows.

American elm *Ulmus americana*
Willow *Salix* sp.
Chokecherry *Prunus* sp.
Narrow-leaved cottonwood *Populus angustifolia*
Broad-leaved cottonwood *Populus sargentii*
Silver poplar *Populus alba*
Cultivated apple *Pyrus* sp.
Wild Plum *Prunus* sp.
Hawthorne *Crataegus* sp.
Lilac *Syringa vulgaris*
Box elder *Negundo* sp.
Alder *Alnus* sp.
Buckwheat *Tiniaria scandens*
Clematis *Clematis ligusticifolia*

In captivity, larvae refused to feed on the foliage of the cork elm and of willow, at least when they had been feeding on chokecherry or apple foliage. They readily turned from chokecherry to apple leaves, and they were even attracted to the apple fruits. Larvae imported from Texas, long after green apple leaves had disappeared at Fort Collins, were successfully reared on slices of apple. In no case were larvae observed feeding on conifers.

Tothill mentions the alder as the favorite host plant in Canada. In the South, the persimmon is often picked out for attack. In Texas and Georgia the webworm's liking for pecan foliage makes it one of the most important pecan pests.

Early defoliation, with production of a tardy crop of fruit usually results in a very poor yield the succeeding year. In the Fort Collins area, successive defoliation of cottonwoods and chokecherry trees must be responsible for the death of many plants.

NUMBER OF BROODS

In general, from New York City southward, the fall webworm is double-brooded. In Colorado and in the northern states and southern Canada, only one brood occurs. Seasonal variation in number of broods has been observed in Nebraska by Bruner (53.)

THE ADULT

The form taken at Fort Collins, Colorado, during the years 1934 and 1935 was pure white on wings and body. The fore tibia were washed with light orange. Dorsally, the shafts of the antennae were covered with white scales. The average wing expanse was three and one half centimeters. Dr. C. P. Gillette states that a spotted form has been taken at Fort Collins, and has been reared from colonies from which the spotless forms were also reared. No spotted adults were seen during the spring flight of 1935.

Emergence

The first moth from a pupa collected in the field and kept in the natural temperature house, issued June twenty-seventh, 1935. It was a male. This was not the first moth of the season. It was reported at lights south of Fort Collins by June the twenty-first. From the fifteenth of June a trap light was run each night near the insectary on the college campus. The first moth, a male, was captured the evening of June twenty-sixth. Thereafter until the evening of July fourteenth, males were taken in the trap in small numbers. Nine were taken on the fourteenth of July, the largest number taken any one night. Not one female was captured in the light trap, and no moth was taken after the fourteenth of July. In the field, the last moths were taken on July seventeenth.

At bright filling station lights, just north of Fort Collins, and particularly five miles south of Fort Collins, on the Denver highway, Hyphantria moths swarmed in considerable numbers. Almost all of them were males. On some evenings they were the most abundant of the Lepidoptera represented. The flight seldom commenced much before nine p.m., and was usually at its height between eleven p.m. and one a.m. On the mornings following a flight the moths were still to be seen about the light, sleeping in the most protected places they could find. In all, only three females were captured at lights. This would seem to indicate that, although attracted by light, the females probably fly less, and depend upon the males to fly to them and fertilize them.

In the light trap records of the Colorado Agricultural Experiment Station there are only two records of capture of H. cunea. The first is July first, 1897, four males; the second, June eleventh, 1898, one female with eggs.

It would seem safe to say, then, that the emergence and flight of Hyphantria moths in the Fort Collins region may begin about the middle of June and last through the first three weeks of July.

THE EGG

The first eggs observed were laid in the laboratory by a female moth captured at a light on July second, and seen in copulation with a male on July fourth. The pair remained in copulo from at least nine a.m. to six p.m. of the same day. They had been placed together on July third. At seven p.m. July fifth, the female had laid her eggs on the under side of an apple leaf in the glass cage, and was still in about the laying position, her wings partly covering the egg mass.

In the field eggs were first found July sixth.

The webworm egg is spherical, the surface covered with many small, low, raised areas, giving it a sculptured appearance. It has been wrongly described as being pitted. The color of the newly laid egg is pale blue-green. This changes to dull yellow or lead color as the embryo develops. Just before hatching time, the brown head capsule of the tiny larva is visible through the translucent egg shell.

The average diameter of twenty eggs selected at random from one egg mass was slightly more than six tenths of a millimeter.

The eggs are probably all laid at one time in a closely packed mass, one layer thick. The female then covers the mass, probably while the eggs are still somewhat sticky, with a thin coating of her abdominal scales. Females that have laid their eggs will be seen to have much shrunken abdomens, almost barren of scales. According to the writer's observations, after laying the eggs, the female rests over them, usually protecting a considerable portion of the mass with her wings. In this position it remains until dead, and a breath of air loosens its hold on the leaf. Many egg masses were collected in the field and only one was found on the upper surface of a leaf. Surely the preferred location for the eggs is on the under surface. The mass is placed, in all cases the writer observed, on one of the terminal leaves of a branch. On the low chokecherry trees, the masses were in the tops. On a large cottonwood tree, the eggs might be thickest in the top, some forty or fifty feet from the ground, but also scattered about at varying heights from the lowest branches upwards, always at the branch tips.

As to the number of eggs laid in one mass, there is much variation. The average number for five egg masses, one laid in the insectary, four collected from canon mouths was three hundred and fifty-six. This figure will be used for the average number of eggs per mass in making estimates hereafter. The writer believes that the webworm nests at the higher altitudes are smaller because of fewer eggs laid. However, egg counts were not made at those points. A number of egg masses were estimated to contain five hundred egg, many had at least four hundred, and a great number of masses probably varied from one hundred and seventy-five to two hundred and fifty eggs per mass. For the region under consideration the figure three hundred and fifty-six is probably about the true average.

As for the number of eggs in the ovaries of female moths, one dissection was made of an individual caught at a light, that, judging from the size of the contained eggs and all other appearances, had never laid an egg. It contained five hundred and twenty-three mature eggs.

Egg Infertility

Almost every webworm egg mass contains eggs which remain pale green, never developing embryos. The cause is generally thought to be infertility. Tothill, in New Brunswick, 1912, found ten percent infertility of eggs. This is a little more than twice that found at Fort Collins during the season of 1935. The number of infertile eggs found per egg mass in twenty-four masses collected over a considerable area in the foothills is given below.

(1.)	6	(13.)	39
(2.)	63	(14.)	25
(3.)	1	(15.)	0
(4.)	8	(16.)	4
(5.)	0	(17.)	61
(6.)	1	(18.)	18
(7.)	3	(19.)	6
(8.)	2	(20.)	73
(9.)	8	(21.)	0
(10.)	0	(22.)	14
(11.)	7	(23.)	7
(12.)	0	(24.)	2
		Total	348

An average of 14.1 infertile eggs per egg mass.

Infertility of webworm eggs is thus seen to be almost exactly four percent.

Length of the Egg Period

The length of the incubation period has been said by various authors to be eight to twelve days. In the insectary, two *Hyphantria* females laid eggs on foliage in their cages under observation, and the lengths of the egg periods were closely determined.

One female laid her quota of eggs between four and seven p.m. July fifth, the day after copulation. The eggs hatched between two p.m. July eighteenth and ten a.m. July nineteenth, a space of something over thirteen days.

THE LARVA

Larval Development

Many thousands of fall webworm caterpillars have been reared in entomological laboratories and by amateur collectors for one reason or another, but in all the literature there are only a few references as to the exact number of larval stadia. Bruner, (53) states that the caterpillars undergo four or five molts. Dyar, (106) who has evidently made the most careful study of the larval growth found seven stadia. His results are given here for comparison with those of the writer which will be presented later.

Head Measurements in Millimeters of two Webworms

Instar	1.	2.	3.	4.	5.	6.	7.
Larva A.	0.3	0.4	0.6	0.81	1.2	1.4	---
Larva B.	---	---	---	----	---	---	2.4
Calculated widths.	0.3	0.4	0.6	0.8	1.2	1.7	2.4

Ratio - 0.7

Snodgrass, (442) believes there are six larval stadia. He figures the first, second, fifth, and sixth instars. While the technique employed by Dyar in his measurements is not known, it is certain that in most of the work, larvae were kept in large numbers in a mass cages, individuals being taken out and measured and described at regular intervals, or whenever the majority was seen to have molted. Either this procedure was too crude to catch the truth or Hyphantria larvae show a greater variation in number of stadia than most lepidopterous larvae. At any rate it will be demonstrated in the following pages that in Colorado Hyphantria normally (the season of 1935 can probably be considered a normal year) has not less than eight larval stadia.

Method of Study

It is probably impossible even to approach duplication of natural conditions in the study of a gregarious caterpillar when the insect is kept alone in an individual cage. In the field, at least during daylight hours, the insect is in close contact with other hairy larvae under the protection of the community web. Undoubtedly the small amounts of heat and moisture and the pressures of neighboring bodies are welcome stimuli to which it responds by remaining snugly in the group. The mass of web allows just the amounts of sunlight and of ventilation to which it has become accustomed through long ages. Any other situation for it, at least in all but the last stadium, is abnormal.

Nevertheless, to make certain that the exact length of each stadium could be determined, and the head width of each instar measured, individual cages were thought to be necessary. A shell vial eight and one half by two and one fourth centimeters was filled to a depth of two centimeters with moist sand. The sand was tamped down and held in place by a disk of heavy blotting paper. The vial was stoppered with a smooth plug of cotton. A fresh apple leaf was cut into a rectangular strip that would fit into the cage, lying with its underside next the glass. This was the sort of cage in which twenty larvae were reared through the first six stadia. The foliage was changed every day for the first instars. The cages were kept in the shaded natural temperature house. It was impossible to lose a molted skin and head capsule in this container except during the process of removing it. Later in the season the almost mature larvae were removed to guaze-covered, tumbler cages, half-filled with sand. After the first stadium was over, each cage was examined at least every three days. If a molt had occurred, the head capsule and skin were placed in a gelatin capsule with a label on which was written the cage number and date. The larva was then placed under a binocular microscope and the width of the head at the widest part determined with the micrometer eyepiece. When the rearing work was completed, the head capsules were sorted, and all those of an individual larva glued in proper order to a microscope slide. They were then measured with probably more precision than could be employed with the live and struggling larvae. These two sets of measurements checked very closely, often to the second decimal place. In the tables of head measurements which follow, the figures obtained by examination of the molted capsules are given unless otherwise indicated.

From time to time, larvae from the mass cages, or from the field were measured to get values for comparison. This practice made it possible to prove beyond reasonable doubt that the experimental results were sound. Under the circumstances this was a worthwhile precaution, for the caged webworms without exception passed through a minimum number of eight stadia, a larger number than any previuusly recorded, and one passed through eleven stadia before dying as a last instar.

On July the eighth, 1935, ten larvae, hatched the day before from a single egg mass, were measured under the binocular microscope and placed by means of a camel's hair brush on a section of apple leaf in individual cages. The first instar was lemon yellow in color except where the green of the intestinal contents showed through the skin. The rather long hairs were whitish or gray except for a few very long ones on the terminal segments which were conspicuously black. But for the dark areas at the bases of the hairs there was no other color on the integument. The head capsule was uniformly dark brown, with darker to almost black mandibles. The head remained brown throughout most of the larval period. During the last two stadia the lower third of the head would often become darker or black. In the fourth instar, a light, narrow, median dorsal line could be discerned, and the darker and longer hairs of the terminal segments disappeared. Not until the last stadium was there a distinct color change. Then, the hairs became suddenly a bright reddish brown.

On July twentieth, another set of ten larvae, recently hatched from one egg mass, was caged like the first. The larvae of the first group all lived through to pupation with the exception of two that died as last instars. Fresh starts had to be made with several of the cages in the second group where death occurred several times among the first instars.

Out of the twenty caged larvae, only ten were content with the minimum of eight stadia. The following table gives the head measurements of each instar for these ten larvae.

Table I.

The Head Measurements of Ten Eight-Stadia Larvae in Millimeters

Stadium - Cage No.	I.	II.	III.	IV.	V.	VI.	VII.	VIII.
35016m	0.36	0.42	0.66	0.96	1.35	1.80	2.40	*2.76
35016n	0.36	0.48	0.60	0.90	1.20	1.71	2.28	2.82
35016o	0.36	0.51	0.69	0.96	1.32	1.86	2.31	*2.82
35016r	0.36	0.54	0.69	0.99	1.35	1.86	2.34	*2.70
35016s	0.36	0.45	0.69	0.90	1.35	1.80	2.34	*2.76
35016t	0.36	0.48	0.68	0.99	1.41	1.86	2.40	*2.76
35016u	0.33	0.45	0.66	0.90	1.34	1.80	2.34	*2.70
35016v	0.35	0.48	0.69	0.93	1.35	1.74	2.22	*2.70
35011a	0.36	0.48	0.69	1.02	1.38	1.83	2.28	*2.58
35011g	0.35	*0.42	0.68	0.93	1.32	1.77	2.34	*2.94
Average	0.35	0.47	0.67	0.94	1.34	1.80	2.32	2.75
Dyar's values-	0.3	0.4	0.6	0.8	1.2	1.7	2.4	

The average ratio between the average head widths was

.74

The following calculated head widths were worked out using Dyar's Law:

Stadium-	I.	II.	III.	IV.	V.	VI.	VII.	VIII.
Head width	0.33	0.45	0.61	0.82	1.11	1.50	2.03	2.75

*Measurements from living individuals only.

The calculations of the head widths for the several instars are seen to check pretty closely with Dyar's own for the first five instars.

The following sets of head measurements were taken from larvae being reared in large mass cages from colonies collected in the field, or from larvae just collected. They are presented with the hope of proving the correctness of the vales in Table I and demonstrating that under natural conditions the larvae pass through at least eight stadia as indicated in that table.

Table II.

Head Widths of Some Larvae in Fourth to Eighth Stadia in Millimeters

Stadium	IV.	V.	VI.	VII.	VIII.
	0.84	1.08	1.44	2.28	2.82
	0.87	1.11	1.53	2.16	2.88
	0.78	1.26	1.44	2.19	2.88
	0.78	1.03	1.50	2.22	2.76
	0.84	1.02	1.50	2.22	2.76
		1.08	1.56	2.16	2.70
					2.82
					2.70
Calculated widths from Table I.	0.82	1.11	1.50	2.03	2.75

It would be surprising, considering the individual differences in the specially cages and systematically measured larvae, if no intermediate widths were discovered in a series of examinations. One larva from a mass cage measured ninety-six one hundredths of a millimeter across the head. According to the calculated values this might be either a fourth or fifth instar. However, it compares very closely with the average figure for the fourth instar which was ninety-four one hundredths of a millimeter.

All the larvae specially caged for head width determinations were supposedly reared under identical conditions. A description of the cages has already been given. However, nine individuals passed through more than eight stadia before reaching maturity, and another died as an eighth instar apparently before maturity. The head measurements of these aberrent larvae are given in the following table.

Table III.

Head Measurements of Ten Aberrant Larvae in Millimeters

Stadium

Cage No.	I.	II.	III.	IV.	V.	VI.	VII.	VIII.	IX.	X.	XI.
35016p	.36	.42	.54	.72	.96	1.32	1.65	2.01	2.28	2.58	3.18
35016q	.36	.51	.72	.93	1.32	1.74	2.22	2.58	3.00		
35011b	.33	.51	.69	.96	1.28	1.62	2.04	2.22	3.06		
35011c	.36	.42	.57	.84	1.14	1.50	1.95	2.46	3.12		
35011d	.36	.48	.69	.98	1.34	1.71	2.16	2.52	2.94		
35011e	.36	.44	.51	.69	.84	1.14	1.59	2.07	(died as immature larva)		
35011f	.36	.51	.68	.84	1.11	1.41	1.92	2.34	2.76		
35011h	.36	.45	.57	.78	1.08	1.44	1.83	2.34	2.40	2.82	
35011i	--	--	.66	.96	1.20	2.22	2.64	(died as immature larva)			
35011j	.36	.48	.69	.93	1.26	1.56	1.98	2.28	2.34	3.12	

These results may indicate two things. First, that under artificial conditions, with perhaps some disturbance of the normal diet, the webworm is capable of passing through more than the normal number of stadia. Second, that a variation in the number of stadia actually exists under natural condtions. Series of measurements of larvae taken in the field during the course of a season would be necessary to determine the truth.

The data in hand, however, surely justify one conclusion, namely, that at least eight stadia are required by webworm larvae for growth to maturity in this region.

Table IV. gives the lengths of the stadia for nine eight-stadia larvae successfully pupating. Table V. gives the same information for three nine-stadia larvae also pupating.

Table IV.

Lengths of Stadia of Nine Eight-Stadia Larvae in Days

Cage No.	I.	II.	III.	IV.	V.	VI.	VII.	VIII.	Prepupa
				Stadium					
35011a	7	4	4	4	6	11	8	19	4
35011g	9	4	6	4	8	7	14	15	3
35016m	7	6	6	4	6	8	11	13	5
35016o	6	5	3	7	6	6	8	11	2
35016r	7	4	6	6	4	6	11	10	5
35016a	6	5	3	7	4	8	8	22	5
35016t	6	6	5	6	4	6	8	13	5
35016u	7	5	5	6	4	6	11	18	5
35016v	6	5	3	7	4	6	10	9	2
Average	6.7	4.8	4.9	9.2	5.1	7.1	9.7	14.4	4.0

The total number of days (average) from hatching to pupation - 65.9 days.

Table V.

Lengths of Stadia of Three Nine-Stadia Larvae in Days.

Cage No.	I6	II.	III.	IV.	V.	VI.	VII.	VIII.	IX.	Prepupa
				Stadium						
35016q	6	5	7	5	6	8	9	8	17	5
35011b	7	4	4	6	10	7	8	16	25	14
35011c	5	6	2	6	4	8	7	13	18	7
Average	6	5	4.3	5.6	6.6	7.6	8	12.3	20	8.6

The nine larvae whose stadia lengths are given in Table IV., considered as a group, hatched by July seventeenth and pupated by September twenty-fourth. These larvae all had eight stadia. One aberrant larva died as a last instar in the eleventh stadium on October fifteenth. One nine-stadia larva did not pupate until October twenty-fifth. Another nine-stadia larva died as a prepupa October twenty-ninth. This last larva was the very latest webworm seen alive in the cage material or in the field exclusive of the pupae.

It is much more difficult to follow the different stadia in the field, due to the fact that larvae are hatching over a considerable period of time, and the webworm population in any area is probably never composed of individuals of one stadium at one time. However, the study area was visited at least once a week, and the size of the larvae noted and compared with that of the caged larvae. This led to the recognition of eight stadia. During the 1935 season the larval period began by July sixth and ended with a few stragglers by October seventh, a space of ninety-four days. This is about twenty-eight days longer than the average larval period for the nine specially caged eight-stadia larvae. The following chart is an attempt to show graphically the duration of the eight larval stadia as determined by field observations.

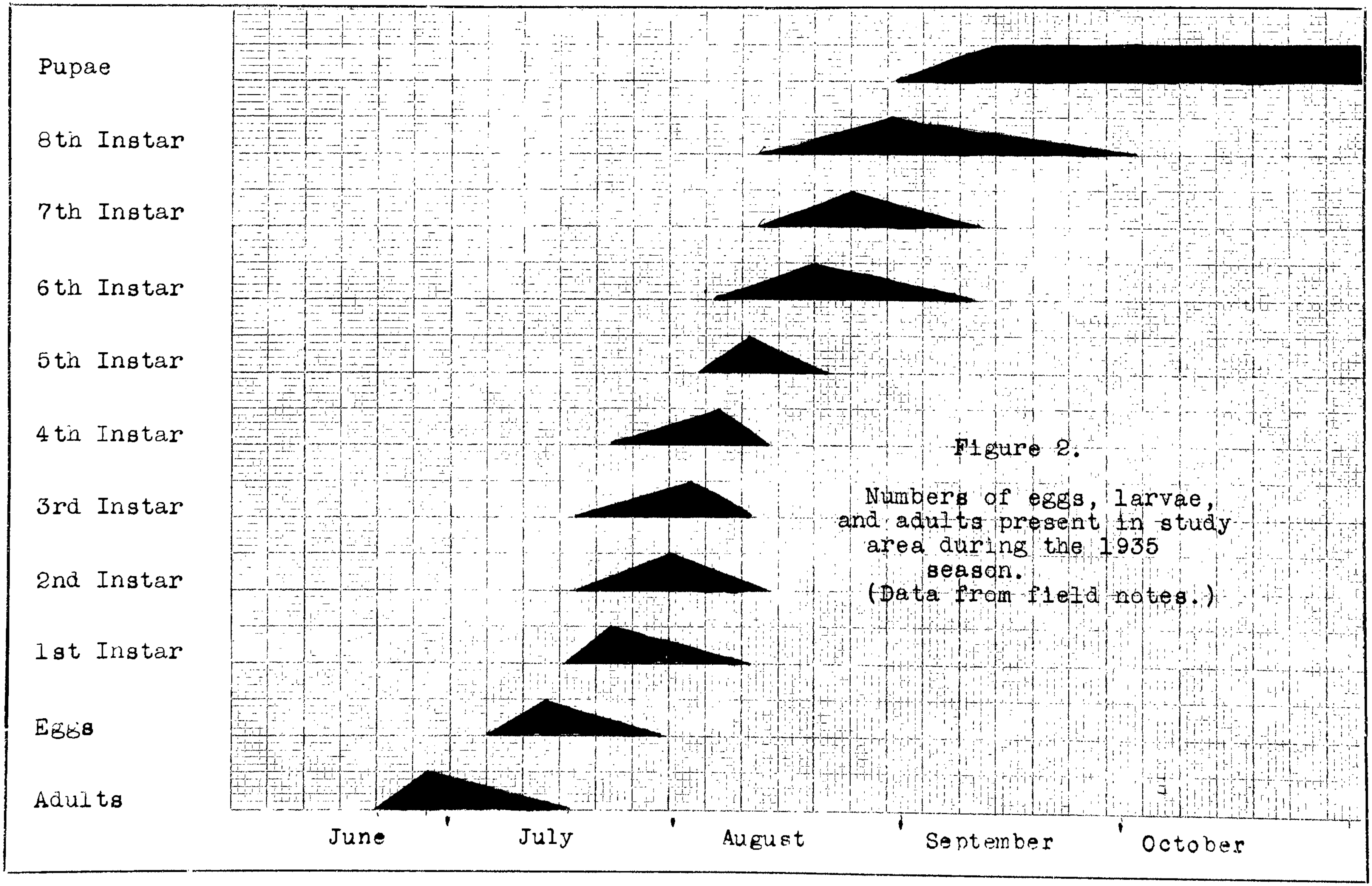


Figure 2.

Numbers of eggs, larvae, and adults present in study area during the 1935 season. (Data from field notes.)

Larval Behaviour

The webworm larva is normally a nocturnal feeder. Under the twilight conditions of the large, cloth-covered, mass cages and possibly under the pressure of hunger, larvae in the insectary fed to some extent during the daylight hours. This nocturnal habit is probably a safeguard against parasites. Many tachinid flies will oviposit only in warm sunny weather. The hymenopterous parasites are probably diurnal. At night, then, the larvae may safely leave the protection of the web to feed and to extend the web itself.

The larvae in the first to third stadia feed from the upper surface of the leaf, devouring the tissue down to the lower epidermis, excepting the tougher vascular portions. Toward the latter part of the third stadium they begin to eat entirely through the leaf, leaving only the larger veins and the petioles. Before the colonly is forced to move to a different branch or to a new plant, all green parts may be devoured. In some cases, the newly hatched larvae were observed to consume most of the egg shells, but in general the egg shells and infertile eggs could be found almost entire on a terminal leaf of an infested branch.

L. M. Peairs (347), observing a colony of webworms, noted that at intervals of from three to five minutes each worm raised the anterior half of its body and rapidly jerked it from side to side at the rate of about forty times a minute. These periods of motion lasted from forty-five seconds to more than a minute. Peairs did not advance any reason for this behaviour but believed it to be habitual.

This is undoubtedly the phenomenon which Tothill calls the "parasite alarm." Any sudden pressure on the web of a Hyphantria colony will set the larvae to waving their heads. It may well be a defense mechanism as Tothill believes. The larvae are in a compact mass in the center of the web. When they rear their heavily chitinized heads and wave them rapidly over the posterior parts of the worms directly in front and to the side of them they must to some extent frighten an attacking parasite. The taut strands of the web are seen to behave a a fairly efficient communication system, spreading the "parasite alarm" by their vibrations to each individual of the colony. This movement does not seem to be exactly periodic. A jarring of the web seems to be the stimulus for the head wagging, which will continue for a brief or considerable period of time depending upon the intensity of the stimulus.

During the molting process, the larvae are exceedingly quiet. Feeding stops, and the larvae mass together in the center of the web. Eighth instars were seen to remain quietly in the web for several days after molting.

Seventh stadium larvae on apple foliage.

Figure 3.

Dorsal view of pupa.

(1½ times natural size.)

Photos by Grant Eddy.

Figure 4.

Then they would disappear from the web and travel away in search of suitable places for pupation. Some feeding is probably done during the migration, for caged eighth instars fed heavily on the foliage supplied them.

THE PUPA

The webworm pupa is dark reddish-brown in color, with a distinctive swelling of the body in the central region. It measures in the female about fifteen millimeters in length and five millimeters across the middle. The male pupa is usually shorter by two to four millimeters.

Pupation

The last instar webworm, on leaving the community web, commences a pilgrimage of uncertain length in search of a place for pupation. This may be any one of many different situations, a brush-pile, a rock pile, in humus, a hollow tree, or under the dead bark of a tree or stump. The larva may be alone or with any number of other larvae when the time for pupation arrives. The long body hairs are used in constructing the light cocoon. Through the walls of this flimsy case the prepupa is easily seen. After the cocoon is prepared there follows a prepupal period of about three days. The last larval skin is then shed and the pale, amber pupa is exposed. The pupa rapidly darkens to a deep reddish-brown and is ready for the long wait of eight or nine months till time for emergence.

THE SEX RATIO

The sex ratio in Hyphantria appears to be about 1:1. Table VI. lists the counts of male and female pupae from five different cages in the insectary. Out of a total of two hundred and forty-eight pupae, exactly Half were male, half female.

Table VI.

Counts of Male and Female Webworm Pupae

Cage No.	No. Pupae	Males	Females
35038	53	25	28
35071	92	44	48
35037	31	18	13
35035	31	20	11
35042	41	17	24
Totals	248	124	124

SUMMARY OF HYPHANTRIA LIFE HISTORY DATA

From the preceding observations on the life history of the fall webworm some general conclusions may be drawn as to the situation in the field during the 1935 season.

Emergence of adults may have begun by June fifteenth, with the peak of emergence from the twenty-first of June to the first of July, approximately. The last adults were seen July seventeenth. Egg-laging was in full progress by the fourth of July. The last eggs were collected July twenty-ninth, when no adults were in evidence. The average number of eggs per egg mass was three hundred and fifty-six, the average diameter of the egg was six tenths of a millimeter. The length of the egg period probably varies from ten days to two weeks. Hatching began about the sixteenth of July and was over by the ninth of August. The larvae passed through at least eight stadia, the last of which was the longest and was the period of migration to winter quarters. The last larva was seen in the field on October second. Pupation commenced by August thirtieth in the field and was at its height from the tenth to the fifteenth of September.

C. THE BIOLOGICAL CONTROL OF THE FALL WEBWORM IN COLORADO

The area in which field observations of the webworms were made has been described. It was in this same area that data on the more obvious natural control factors were collected.

Climatic factors, temperature, humidity, precipitation, and wind movement must directly affect host, parasite, and predator populations. It must then also have indirect effects upon each population due to consĕquent increase or decrease or stability of these groups.

In order to guage intelligently the influence of climate upon the webworm populations of 1934 and 1935 at Fort Collins, it would be necessary to have climatological data over a period of many years. This was not available. However, these things are known: the past five years in Colorado have been years of unusually low precipitaion with mild winters. The winter of 1934 was exceedingly mild with long periods of warm sunny weather. With the greater abundance of water in the canons of the foothills, the food supply of the insects was probably not greatly affected by the general drouth. On the whole, the effects of climate upon the webworm population have certainly not been striking and have been almost unvarying for at least five years.

The increase in webworm population from 1934 to 1935 has already been remarked. The amount of increase was not and could not be determined by counts of webs. In Canada, Tothill estimated the scarcity and abundance of webworms by counting the webs along a measured stripoof road. In the study area at Fort Collins, where groups of trees were completely stripped of leaves, counting individual webs would be almost impossible. In the tops of badly infested cottonwoods great numbers of egg masses were laid. Soon after hatching larvae of one colony were forced to mingle with those of others. The branches became filled with the webs, and colonies could not be distinguished. A count of defoliated trees of a certain species or size might have given a fairly accurate measure of the amount of increase. By observation of the infestation along the canon roads in the study area a thirty to fifty percent increase in the webworm population was roughly estimated.

RESULTS OF THE 1934 FIELD WORK

Collecting in 1934 did not commence until mid-September, when the webworms were already pupating. Webs contained only straggling eighth instars with a few belated seventh and sixth instars. However, the Meteorus and Hyposoter parasite cocoons were still hanging in the webbing. Many webs were therefore gathered and brought to the insectary for examination. The parasite cocoons were picked out, and those without the exit holes of the maker or of hyperparasites were placed in individual vials with cotton stoppers. A number of these whole parasite cocoons were brought into a heated building to hasten issuance of the adults. Others were left in the natural temperature house. Only a very few Hyposoter and Meteorus adults issued from the collected material. The issuing data will be considred in the accounts of the individual parasites. What are to be presented here are the conclusions that were drawn as to the percentage of hyperparasitism.

Number of Hyposoter pilosulus cocoons collected ..	863
of which 451 (52.1%) were parasitized.	
Number of Meteorus acronyctae cocoons collected ..	91
of which 26 (28.4%) were parasitized.	
Number of Phorocera floridensis puparia collected.	3
Number of other dipterous puparia	2
Number of braconid cocoons collected	56
of which 17 (30.3%) were parasitized.	
Number of other ichneumonid cocoons	8
Total number of parasite cocoons..............	1023

In the following pages the parasites and hyperparasites reared from Hyphantria during the 1935 season are discussed individually.

THE PRIMARY PARASITES

Egg Parasitism- Trichogramma minuta Riley

Twelve egg masses were collected from the Redstone and Buckhorn Canon regions from July seventh to twenty-ninth and brought to the insectary where the eggs hatched. No egg parasites issued. Egg mass remains from some fifty colonies collected from all parts of the study area were carefully examined under the binocular microscope for traces of parasitism. Of these only one was parasitized. In this instance the eggs from which the larvae had just hatched were placed in a cotton-stoppered vial on July seventeenth. Examination on August eighth revealed that one male and three female hymenopterous egg parasites had issued and died in the vial. Two others had died while attempting to issue. Four eggs contained the small round parasite exit holes besides those from which the dead adults had emerged, and four other eggs contained the dead bodies of larval or near-adult parasites.

The dead adults were mounted in balsam and sent to the United States National Museum. Mr. A. B. Gahan, there, determined them as _Trichogramma minuta_, stating in part - "The parasite---from eggs of _Hyphantria cunea_ is _Trichogramma minuta_ Riley as I interpret the species. it is one of the dark forms which may or may not be a distinct race or variety of the species." The writer has not found this species recorded as a parasite of the fall webworm in the literature. The percentage of egg parasitism is obviously so small as to be negligible.

Two hymenopterous egg parasites have previously been recorded from *Hyphantria* :-

Trichogramma pretiosa Riley (Tothill, 1922)
(Superfamily *Chalcidoidea*)

Telenomus bifidus Riley (Riley, 1887)
(Superfamily Proctotrypoidea)

Neither species has apparently ever been responsible for any consederable percentage of egg destruction.

Meteorus acronyctae Muesebeck

This braconid primary parasite is here recorded for the first time from *Hyphantria*. It is the most important parasite in point of numbers after *Hyposoter pilosulus*.

Meteorus acronyctae Mues. was described from Hell Canon, New Mexico, in Proceedings of the United States National Museum Volume sixty-three, article two, pages thirty-seven to forty, 1924. *Acronycta* (*Noctuidae*) and *Euschausia* (*Arctiidae*) are named as hosts. It will be seen that several of the primary and secondary parasites of *Hyphantria* at Fort Collins belong to the southwestern fauna.

The cocoons of *M. acronyctae* are spun outside the host. After leaving the dying caterpillar, the parasite spins a thread perhaps five to eight centimeters long and at the end of it constructs a hard-walled, brown cocoon. It is cylindrical, tapering at both ends, and is about five millimeters long. Clusters of these swinging brown cocoons are conspicuous objects in the Hyphantria web.

Probably only one individual of this species normally matures from a single webworm. However, two larvae were observed leaving a webworm at one time. Both spun cocoons and emerged as adults.

The first adult seen in 1935 issued August twentieth from webworm material collected July twenty-second. The webworms were mostly in the fourth stadium. But the mass of Meteorus from this group of caterpillars issued about September thirteenth, and one did not issue until October seventh. The insect that emerged on August twentieth was found in cocoon on August ninth.

A Meteorus larva was observed leaving its host webworm at three p.m. August twenty-ninth. In forty-five minutes the larva was completely enclosed in a strong, light net of silf, and work upon the interior was well under way. This insect had emerged by September nineteenth, spending about twenty-one days in its cocoon.

Before September first, the average number of Meteorus cocoons per webworm colony was two and two-tenths . This number increased to four and two-tenths after September first. This nearly one hundred percent increase in number of coons might seem to indicate two generations of the parasite upon *Hyphantria*, but other observations indicate only one. *Meteorus* adults, emerging in the insectary, could not be induced to oviposit in webworms. The last *Meteorus* emerged October fourteenth in the insectary, and dissections of cocoons thereafter showed that the occupants were dead or parasitized.

Since this was a later-appearing insect, secondary *Hyphantria* parasites preyed upon it almost from the first. Material collected as early as August fifth had been parasitized by *Dibrachys cavus*.

Of the four hundred and eighty-one *Meteorus* cocoons collected during the 1935 season, two hundred and twenty-five, or roughly forty-seven percent, were parasitized. For the season, *Meteorus* averaged six and four tenths per webworm colony, a parasitism of one and eight tenths percent.

Apanteles hyphantriae Riley

Adults of this braconid species were not reared from collections at Fort Collins. However, cocoons closely resembling those of *A. hyphantriae* were collected in the fall of 1934. From them a number of secondary parasites had issued.

On October fifth, 1935, five colonies of webworm larvae in the third to fifth stadia were collected from pecan at College Station, Texas, and sent to Fort Collins. They were placed in large, screen-cloth cages and reared to maturity. Only one colony showed parasitism, and this was by Apanteles hyphantriae, determined by Mr. Muesebeck. The percentage parasitism was a little more than ten percent.

Hyposoter pilosulus Prov.

At Fort Collins, the ichneumonid H. pilosulus is the most important primary parasite of the fall webworm. A series of specimens of this species was determined by Mr. A. B. Gahan. Since a determination of the webworm population in 1934 could not be made, the percentage of parasitism due to this species that year could not be estimated. However, the hyperparasitism of H. pilosulus was found to be fifty-two and one tenth percent. In 1935, with the rearing of whole colonies of webworms in the insectary, and the determination of population of the average webworm colony, the percentage of parasitism could be found. In each webworm colony of three hundred and fifty larvae (the figure obtained by subtracting the percent of infertile egg from the total number of eggs laid), H. pilosulus was responsible for the death of eighteen and six tenths larvae on the average, five and three tenths percent of the total population.

Hyposoter cocoons are easily found. The parasite spins its cocoon inside the skin of its larval host, which may be in any stadium from the fourth to the eighth. The cocoon itself is thus not visible, but the skins of the dead hosts, bloated anteriorly, where the parasite cocoon lies, and shrunken otherwise, are conspicuous objects hanging in the mesh of the webbing or adhering to the trunk or branches of infested trees.

The first adult *Hyposoter* was observed in the field on August eleventh. Itwwas a female, and it was in the midst of a web of *Hyphantria*, forcing its way through the impeding strands of silk, attempting to sting the sixth stadium larvae. Twice it was seen to get in stinging position and make vicious thrusts at a fleeing larva, but each time it failed to drive its ovipositor home. Then, alarmed at efforts made to capture it, it escaped from the web and flew away.

It has been observed by various writers that oviposition in this parasite usually occurs in the last few segments of the host caterpillar. This has usually been attributed to a preference on the part of the parasite for this particular portion of the host, the caudal region being less active, and not armed with jaws or heavily chitinized areas. But another explanation seems more reasonable. The larva about to be attacked is usually aware of the approach of its enemy and tries violently to escape. The wasp, being on foot, must run to catch up with it, and the tail of the host is the first part met with. In captivity the act of oviposition was observed hundreds of times. On many occasions, when a stupid larva blundered into a resting wasp, it was stung on one of the first segments of the body. Once the victim even seized the ovipositor of the wasp in its jaws, andd the prisoner released itself with difficulty.

Between July seventeenth and August twenty-fourth, forty entire webworm colonies were collected, brought to the insectary and placed in large cloth-covered cages with apple foliage. At intervals the webbing was examined for cocoons of the parasites. The first cocoons were found August twelfth, when a dozen were removed from the webbing of a cage containing two colonies of webworms. The first adult issued August twelfth. This adult was allowed to oviposit in webworm larvae on the day of emergence. Its first descendent emerged September fifteenth. Thus two generations of the primary parasite are seen to be possible upon Hyphantria.

A decided increase in the numbers of parasite cocoons in webs collected after September first was noted. This was probably due to the appearance of the second generation on Hyphantria. Allowing all cocoons collected before

September first to belong to the first generation of wasps, the average number per *Hyphantria* web was only one and eighteen one hundredths.

From September first to October second, fifty-four whole webs, many of them empty of webworms, were collected and brought to the insectary or were examined in the field. *Hyposoter* cocoons averages eighteen and sixty-six one hundredths per web. Subtracting the average number of cocoons per web before September first, we obtain the figure sixteen and five tenths, which is the increase in parasite numbers per colony due to the second generation. Eighteen and sixty-six one hundredths larvae, the average number of webworms destroyed by *Hyposoter* per colony during 1935, was five and three tenths percent of the three hundred and fifty larvae hatching from the average egg mass.

Rearing Experiments with Hyposoter

Three females of this species issued from webworm material collected from July twenty-second to August twentieth, were used in rearing experiments. The wasp immediately upon emergence was transferred from its narrow vial cage to a larger one about eight and one half by two centimeters. A drop of thick sugar syrup was placed on the side of the vial as food. The vial was stoppered with cotton.

It was into this sort of cage that webworm larvae were placed one at a time to be parasitized by the wasps. The larvae used were usually in the fourth or fifth stadium, the smallest larvae available. Undoubtedly oviposition in the field may take place when the webworms are in the second stadium, as Tothill says it does in Canada. Even eighth stadium larvae were attractive to the wasps, although the longer hairs were a hindrance to oviposition. No wasps were reared from webworms stung in the last stadium. The victim always died or pupated before the parasite larva reached maturity. They were repeatedly reared from seventh stadium larvae.

The wasps readily oviposited within a very few hours after emerging. The attention of a wasp was usually attracted at once by the presence of a webworm in its vial. It would wave its antennae more and more rapidly, then run toward the victim. As soon as its antennae brushed the ends of the hairs of the webworm the wasp would curve its abdomen under the thorax and thrust furiously forward with its ovipositor. The stab received by the webworm usually caused it to squirm and commence to move away, dragging the wasp with it a short distance. The wasp would passively allow itself to be dragged for a fraction of a second, then grab a secure footing and release its ovipositor. The whole act of oviposition required a bare second. Often wasps were observed to oviposit as many as four or five times in a single larva before the latter could be removed from the vial.

Tothill (476), writes that judging from the length of the uterus, only a few eggs could be stored there, and that probably only a few eggs are laid each day over a period of a fortnight by a Hyposoter female. But in one of the present experiments a female oviposited in forty-four larvae in the space of twelve hours, forty-one eggs being laid between seven-fifteen p.m. and nine-thirty-five p.m. of the same day. During this particular evening (the wasp was kept under a strong electric light) the parasite showed no signs of tiring, and stung larvae as rapidly as they were presented, often at the rate of one a minute.

These three females were unmated. As a result, all the progeny were males. Two females were lost after a few stingings. One, issuing September first, lived until September eighteenth, and attempted to oviposit on the second day before death.

Forty-nine male Hyposoter adults were reared from these three parents. The average time from formation of cocoon to emergence of the adult, roughly the pupal period, was eighteen days. The full life cycle, the, under insectary conditions occupied an average of forty-three days. This probably somewhat longer than field conditions require. The last Hyposoter adult issued October seventh from material collected in the field. It is thus seen that there is ample time for two complete generations of *Hyposoter* upon the fall webworm after the first week of July. It also seems likely that there is still another earlier generation on an alternate host. This host, if it exists, might possibly be *Malacosoma fragilis* (see under DIPTEROUS PARASITES below), but no *Hyposoter* were reared from this insect.

Mating

Two matings occurred under observation, but the fertilized females refused to oviposit. One pair were in copulation exactly five minutes. The duration of the other copulation was not noted. The male approaches the female from the rear, seizes its abdomen with the first pair of legs and bends the tip of the abdomen downward to meet that of the female's.

Eight matings, observed by William Green and Roland Portman of this department, lasted an average of five minutes each. A series of experiments were performed by Green, Portman, and the writer in an attempt to determine the sex ratio in progeny of fertilized females. The detailed results are to be published elsewhere, but a preliminary survey of the data stronly indicates a one to one sex ratio.

It is interesting to note that these later experiments were performed with adults of the second generation on *Hyphantria*, a generation that under field conditions would have gone into hibernation. Moreover, the progeny of this abnormal third generation mated and readily oviposited in webworms imported from southern Texas, and a fourth generation was reared in the greenhouse long after the webworms at Fort Collins had pupated.

Hibernation

H. pilosulus almost certainly winters as an adult in such protected places as rock crevices, the interiors of rotten logs, etc. Dustan (104), in Canada, kept adults alive in hibernation cages until March of the next year. These insects died before webworms were at hand for them to parasitize. A number of pupal *Hyphantria*, parasitized in the last stadium, were dissected. In some cases the third or last instar of the parasite larva was found, dead apparently of phagocytosis. Phagocytosis in *Hyphantria* is discussed by Tothill (476.)

Hyposoter fugitivus pacificus Cush.

One male specimen of this parasite issued from a cocoon supposed to be that of *H. pilosulus*, on October fourteenth, 1935. It was determined by Mr. Cushman.

Elachertus hyphantriae Crawford

This little eulophid, a member of the superfamily Chalcidoidea, was described by Crawford in the Proceedings of the United States National Museum Volume thirty-nine, 1911, from specimens reared from webworms at Cuero, Texas. In Dixon Canon, on August eleventh, 1935, six webworms bearing naked black hymenopterous pupae about two millimeters in length were collected, two from the same colony, and brought to the insectary. The host larvae were all in the fifth or sixth stadia. The pupae of the parasites were all located about exactly in the middle of the backs of their hosts. The hosts, very sluggish, were placed in individual vials with food. By August thirty-first, four adults had issued and died in the vials. The host larvae were also dead. Mr. A. B. Gahan determined the parasites as Elachertus hyphantriae Crawford.

The Dipterous Parasites

The known dipterous parasites of Hyphantria are all members of the family Tachinidae, all probably ovi- or larvipositing in the caterpillars. According to the work of Tothill in Canada, and the government gipsy moth laboratory in this country, the tachinids are never responsible for a very high percentage of parasitism. They may be fairly numerous one season, and practically disappear the next. They should probably be considered among the less important primary parasites. At Fort Collins, two tachinids, one not previously known from *Hyphantria*, were reared

Phorocera floridensis Townsend

During the fall of 1934, five tachinid puparia were found in cages containing *Hyphantria* larvae. Only one adult issued. The puparium of this fly was found on the soil surface in a cage containing webworm pupae and dead larvae. The fly issued October fifth. The host was not found. Dr. H. J. Reinhard determined the parasite as *Phorocera floridensis* Townsend.

On September twenty-fourth, 1934, a *Hyphantria* larva, collected on the twentieth of September was placed in an individual cage with a soil bottom. This cage was not examined until October eleventh, 1934. On the side of the glass was the typical hair cocoon of the webworm. It contained a partly devoured prepupa. On the surface of the soil in the cage was a little pile of loosened earth. Half an inch below this was a large, purplish puparium, very probably of *Phorocera*. The adult did not issue. Another *Phorocera* (?) puparium was found hanging in the webbing of a colony of webworms collected September seventh. The puparium was discovered on September twenty-eighth. The adult did not issue.

During the summer of 1935, a *Hyphantria* pupa from the previpus year was opened. It contained a large puparium, dead, probably of Phorocera.

Two smaller puparia were found on soil in Hyphantria cages in 1934. Judging from their size and appearance they were of a different species. Adults did not emerge.

In 1935 only one tachinid species was collected. It is the next parasite to be described. Thus for two years, at least, in the study area, dipterous parasitism has been of very little impportance in the control of the fall webworm.

P. floridensis was described as a new species under the genus Euphorocera by C. H. T. Townsend in Entomological News, Volume twenty-seven, page two hundred and seventeen, 1916. The holotype was reared from Anticarsia gemmatilis Hübn. at Gainesville, Florida. Aldrich and Webber, in Proceedings of the United States National Museum, Volume sixty-three, article seventeen, page sixty, 1923, give a longer accoutn of this species, adding the hosts Plathypena scabra Fabr., Saperda sp., Taphygma frugiperda A. & S. and extending the known range of the species north to North Carolina, west to Arkansas, and south to Costa Rica.

Zenillia blanda virilis A. & W. - Seasonal Alternation of Hosts

When beginning the study of the parasites of the fall webworm, it was thought necessary to consider possible alternate hosts. This seemed especially necessary since Hyphantria larvae would not be available for parasitism until July, while both hymenopterous and dipterous parasites might issue long before. Therefore the study area was searched for lepidopterous larvae of habits similar to those of Hyphantria. Two species were found, Malacosoma fragilis Stretch, the western tent-caterpillar, and Archips cerasivorana Fitch, the cherry tree tortrix, both web-spinning, gregarious caterpillars. The former was the earlier-appearing species.

Malacosoma was not abundant in the study area during 1935, although in some parts of the state it was causing serious damage to aspen forests. The first collection was made June twenty-fourth. At this time the larvae were a little over half-grown. The thick webs were mostly on the low-growing Rhus trilobata on the eastern slopes of the lower foothills. Several species of hymenopterous parasites and secondary parasites were reared from the larvae, but none of them appeared later on Hyphantria.

Archips was especially prevalent in a wide valley near Masonville, Colorado, where choke cherry and wild plum grew in dense thickets. In this valley Hyphantria was abundant. The webs of *Archips* on choke cherry at this time, July sixth to fifteenth, were filled with mature larvae and pupae. A number of the webs were brought to the insectary and placed in cages. On July twentieth, tachinid puparia were first observed on the floors of the cages and in the webbing. The fly larvae had left the moth pupae and pupariated in the masses of frass or on the ground. By August fourth, the first adult tachinids had issued. They were sent to Dr. Reinhard, who determined them as *Zenillia blanda virilis* A. & W.

The host, *Archips* emerged during the next week or two and laid eggs for overwintering.

Zenillia was not observed again during the summer. On January thirtieth, 1936 a box containing some *Hyphantria* pupae, kept since early fall at room temperature, was opened. It contained an adult tachinid, issued perfectly, but dead. The empty puparium and host pupa were found. Dr. Reinhard identified this specimen as *Z. blanda virilis*. The host pupa was reared from a larva collected September eleventh near Masonville. Under field conditions the tachinid would not have issued until spring.

This is probably a case of true seasonal alternation of hosts. *Zenillia*, if it is regularly parasitic upon *Hyphantria*, issues from the pupae in the spring and parasitizes *Archips* larvae. The adults of the first generation then victimize young hyphantrians, no more

Archips larvae being available. No other parasites or secondary parasites reared from *Archips* were reared from *Hyphantria*.

It seems likely that a number of the parasites and secondary parasites of *Hyphantria* have another earlier-appearing host.

Zenillia blanda virilis was first described by Aldrich and Webber in Proceedings of the United States National Museum, Volume sixty-three, article two, page forty, in 1924. It has been collected in New York and Kansas. The known hosts at time of description were *Papaipema harrisii* Grote and *Ennomos subsignarius* Hübn.

THE SECONDARY PARASITES

Hemiteles tenellus Prov.

This ichneumonid is a secondary parasite of minor importance at Fort Collins. It was reared in about equal numbers from H. pilosulus and M. acronyctae. By October fourteenth, 1934, ten Hemiteles had issued from Hyposoter cocoons collected on the fifteenth and twentieth of September. This was no indication of the abundance of Hemiteles during the entire season.

In 1935, Hemiteles did not appear until October. The period of emergence began October first and appeared to end October twenty-sixth. During this time, twenty-six adults emerged in the insectary, eighteen from cocoons of Meteorus, thirteen from cocoons of Hyposoter. After another month had passed, it was thought no more Hemiteles would issue. But late in November the parasite cocoons were all removed from the natural temperature house to the greenhouse, where the temperature did not fall below sixty degrees Centigrade, and ranged upward during the day to about eighty degrees Centigrade. On Janyary twenty-second, 1936, a female Hemiteles issued from a Meteorus cocoon. On February eighth, two more females issued, also from Meteorus cocoons. It thus appears that Hemiteles may overwinter in cocoons of Meteorus and possibly Hyposoter in the field. It seems likely that there is an earlier alternate host.

The Hemiteles material was determined by Mr. R. A. Cushman.

Gelis utahensis Strick.

Two wingless females of this interesting ichneumonid were reared from cocoons of H. pilosulus. One of them emerged February third, 1936 from a cocoon collected September eleventh, 1935. The cocoon had been in the greenhouse more than two months. The Hyposoter host was dead and partially devoured as a third stadium larva. The Gelis larva had spun a thin white cocoon inside that of its host. The other Gelis adult emerged about mid-November without having been in the greenhouse at all. The weather up to time of emergence had been very mild, and the cocoon was in a protected place in the natural temperature house. From these data one might conclude that Gelis hibernates inside the host cocoon in the Hyphantria web as an adult, or during late warm spells emerges and seeks other quarters. In any case it is a secondary parasite of very minor importance at Fort Collins. One specimen was determined by Mr. Cushman.

Perilampus hyalinus Say

This beautiful perilampid was reared only twice during 1935, both times from H. pilosulus. The specimens were determined by Mr. Gahan.

A collection of webworm larvae made August eleventh yielded an H. pilosulus cocoon by September twenty-eighth. From this cocoon a Perilampus adult emerged November fifth. The second specimen emerged November twenty-eighth from an H. pilosulus cocoon collected September fourteenth.

Both of the ichneumon cocoons mentioned had been kept in the greenhouse for about two weeks before emergence of the secondary parasites. It seems likely that the adults may hibernate inside the protecting cocoons of their hosts. This would account for the fact that an adult would emerge late in November after a short exposure to greenhouse temperatures.

Hypopteromalus percursor Gir.

This brilliant green pteromalid was reared in about equal numbers from H. pilosulus and M. acronyctae during the fall and winter of 1935-1936, fourteen from the former, fifteen from the latter. Cocoons of H. pilosulus from the 1934 season collected February fifth, yielded Hypopteromalus adults on June eighteenth and twentieth of 1935. These cocoons were held in the insectary at temperatures close to those in the field. It is evident that this species may remain in the host cocoon throughout the winter and spring, emerging at least near to the time of appearance of Hyphantria larvae.

In 1934, two adults of this species had emerged by September twentieth. In 1935, none emerged before October fourteenth, and most of them did not emerge until January and February even through kept some two months in the greenhouse.

Very probably, then, there is but one generation of Hypopteromalus at Fort Collins, at least as a secondary parasite of H. cunea, but adults may emerge in the late fall or not until the following spring.

Mr. Gahan determined this species and also Hypopteromalus sp. Only a single specimen of the latter is known to have been reared. H. percursor, at present is a secondary parasite of small importance at Fort Collins.

Dibrachys cavus Walker

This pteromalid was the secondary parasite next in importance after Catolaccus aeneoviridis. A series of this species was determined by Mr. Gahan. It is apparently a normal superparasite. The average number of individuals reared from twenty-one Hyposoter cocoons was slight over six. It varied from one to fifteen.

Dibrachys was responsible for fourteenand five tenths percent of the secondary parasitism of Hyphantria. Ninetythree individuals were reared or dissected from *Hyposoter* cocoons and thirty from *Meteorus* cocoons.

A webworm larva collected August fifth, yielded a *Meteorus* cocoon by September second. On October fourth, two *Dibrachys* adults had issued. This indicates that *Dibrachys* oviposits in the webworm larva, or that the parasite larva enters the webworm and perhaps lives in it for a longer or shorter period of time waiting for an opportunity to enter its own host, a *Meteorus* or *Hyposoter* larva.

Like *Catolaccus*, next discussed, this species emerged over a space of several months under greenhouse conditions. Until the first week of October, none had emerged from primary parasite cocoons, reared or collected. From November on, when the host cocoons had all been removed to the greenhouse, adults emerged from time to time until March. At date of writing (March 5, 1936) there are still live *Dibrachys* larvae in the greenhouse. In the field, winter is evidently passed as larvae or pupae inside the host cocoons, or perhaps as adults.

Catolaccus aeneoviridis Gir.

This little pteromalid, a series of which was determined by Mr. Gahan, was the most important secondary parasite of *Hyphantria* at Fort Collins. It parasitized *H. pilosulus* and *M. acronyctae*. About three times as many were reared from the former as from the latter. The actual numbers reared were four hundred and ninety-six from _H. pilosulus_ and one hundred and sixty from _M. acronyctae_. Alone, _Catolaccus_ was responsible for seventy-seven percent of the secondary parasitism.

This insect hibernates inside the cocoon of its host in the _Hyphantria_ web. Adults emerged almost every day in the greenhouse from October through March. Dissections of cocoons in January showed pupae and larvae to be in about equal number. The host dies in either the larval or pupal state. The parasite is usually found inside a very thin cocoon, though often no trace of a cocoon is present. It would appear that winter is passed as either larva or pupa.

No direct evidence of more than one generation was found, but this may have been due to the scarcity of the first generation of primary parasites. Cocoons from which _Catolaccus_ were thought to have emerged were collected on September fourteenth. Adults were seen flying about the _Hyphantria_ webs on the same date. These individuals emerging in the fall may have been ovipositing and may have been of an earlier generation. Or they may have been individuals doomed to die or to hibernate as adults.

Accidental superparasitism was not uncommon. Never more than two _Catolaccus_ were reared from one _Hyposoter_ cocoon. Superparasitism did not occur in _Meteorus_, probably because of the smaller food supply.

TERTIARY PARASITISM

Tetrastichus doteni Crawford

This was the only tertiary parasite reared at Fort Collins, and is here recorded for the first time from Hyphantria. The material was determined by Mr. Gahan. Tetrastichus was reared from cocoons of Hyposoter pilosulus and Meteorus acronyctae. It parasitized Catolaccus and Dibrachys, but so far as is known did not attack Hypopteromalus. Adults emerged from both larval and pupal forms of the secondary parasites. In one case, eight Dibrachys pupae in a Hyposoter cocoon were all parasitized. Where the secondary parasite was Catolaccus, only one individual survived. It has been shown that oviposition in Dibrachys probably occurs in the webworm larva. This must also be true of the tertiary parasite. During 1935, twenty-five Hyposoter and seven Meteorus cocoons containing Tetrastichus were taken. There is evidence of only one generation upon Hyphantria. A Hyposoter cocoon taken September fifteenth, 1934 and kept at room temperature yielded an adult T. doteni four and a half months later. Another taken September twentieth, 1934, and kept at outside temperatures till January first, then at thirty degrees Centigrade, yielded an adult May fifth, 1935. A third, taken in February 1934 and kept at outside temperatures, yielded an adult June twenty-four, 1935. Thus the hibernation period may be a prolonged one.

SUMMARY OF PARASITE DATA, SEASON OF 1935

Parasitism by H. pilosulus 5.3%

" " M. acronyctae........................ 1.8%

Total primary parasitism............ 7.1%

Cocoons of H. pilosulus reared and collected... 1008

Parasitized by	Catolaccus...........	496	
" "	Dibrachys	93	
" "	Hypopteromalus......	14	
" "	Hemiteles	13	
" "	Perilampus	2	
" "	Gelis	2	
		620	(61.5%)

Cocoons of M. acronyctae reared and collected... 481

Parasitized by	Catolaccus...........	160	
" "	Dibrachys	30	
" "	Hypopteromalus......	15	
" "	Hemiteles	20	
		225	(47%)

Total number of primary parasites... 1489

" " " secondary parasites.. 845

Secondary parasitism is 56.7% of the number of the primary parasites.

Total number of teritary parasites ... 32

Tertiary parasitism is 3.7% of the number of the secondary parasites.

FUNGUS DISEASES OF HYPHANTRIA LARVAE

Riley (377), remarks on the large number of *Hyphantria* larvae killed in Washington, D. C. by a white, mealy fungus, seemingly a variety of, if not the same fungus attacking the commercial silkworm. Pupae in cocoons were also affected by the fungus, and even the cocoons of the parasite *Apanteles hyphantriae* were found to be diseased. Riley believed the fungus to be a variety of *Botrytis*.

Atkinson (5), states that *Empusa grylii* Fresenius was responsible for an epidemic of fungus disease among *H. cunea* larvae in Washington, D. C., apparently referring to the outbreak described by Riley.

Garman (175), observes- "The most useful natural agent here in Kentucky is one of the parasitic fungi, *Empusa grylii* form *aulicae* which destroys myriads of the caterpillars (*H. cunea*) ...I am inclined to believe that not less than fifty percent of the second brood in eastern Kentucky in the summer of 1890 were destroyed by this fungus."

No fungus disease among webworms either in the field or in the insectary was recognized at Fort Collins.

WILT DISEASE

Wilt disease, sometimes called nuclear disease or Polyederkankheit, is reported from **Hyphantria** by Chapman and Glaser (67). No larvae suspected of having wilt disease were observed in the field. A number died in the mass cages which exhibited some symptoms of wilt. No examination for polyhedral bodies was made.

PREDATORS

A number of different animals have been reported as being predatory upon Hyphantria. They may be divided into three groups, birds, insects, and arachnids.

Few birds feed regularly upon hairy larvae. The cuckoos often destroy great numbers of tent-caterpillars. It is probably that they will eat webworms. In Canada, the red-eyed vireo, Vireosylwa olivacea L.,has been a very efficient destroyer of webworms. The importance of this bird in webworm control is discussed at length by Tothill (476). Screech owls have been known to eat quantities of webworms. It is likely that many birds will devour a webworm moth on occasion.

In the study area there were probably no birds feeding by preference upon hairy caterpillars. Many of the more common species were seed-eaters. Birds were at no time seen to feed upon webworms at Fort Collins.

Many species of spiders will eat wandering webworms. Some, however, appear to be attracted by the colonies themselves, and will live almost entirely upon the larvae during the course of an outbreak. Two species have been recorded as showing a special liking for webworms. These are _Marpessa undata_ and _Attus tripunctatus_. A few small spiders were noticed in _Hyphantria_ webs in the study area. They may have been feeding on small larvae. In general they were not numerous enough to be control factors of importance.

The most important class of predators is probably the insects. In the _Carabidae_ of the _Coleoptera_, _Plochionus timidus_ Hald., has been recorded several times as an enemy of the webworm. In the _Orthoptera_, the preying mantis sometimes takes numbers of webworms. The most effective predators are probably found among the _Hemiptera_. The following species are redorded as webworm destroyers:-

Podisus serieventris Uhl.

Podisus maculiventris Say

Euschistus servus Say

Arilus cristatus L.

At Fort Collins, several nymphs of an undetermined pentatomid were found feeding on the larvae. Their scarcity in the study area would make them very minor control factors.

SUMMARY AND DISCUSSION

It has been found that in the northern foothill region of Colorado, *Hyphantria cunea* is a single-brooded form, emerging from the hibernating pupae from mid-June to mid-July. The sex ratio is probably one to one. Oviposition begins soon after emergence. A single female lays an average of three hundred and fifty-six eggs in a compact, single-layered cluster, usually on the undersides of the terminal leaves of a variety of deciduous trees. The eggs begin to hatch by mid-July, the last probably hatching by the end of the first week in August. The gregarious larvae pass through at least eight stadia. During September, larvae in the last stadium leave the community webs and wander to protecting crevices in rocks, stumps, or brush heaps, there to make their frail cocoons and pupate.

It has already been stated that *Hyphantria cunea*, at Fort Collins, showed an increase of at least thirty percent in population from 1934 to 1935. This was to be expected, knowing that less than ten percent of the larvae were destroyed during the 1935 season by the primary parasites, the major control factors, and that the mortality due to the same cause in 1934 could not have been much higher.

The primary hymenopterous parasites were found to be by far the most important control factors at Fort Collins. Of these insects, two ichneumonids, Hyposoter pilosulus Prov. and Meteorus acronyctae Mues. were responsible for most of the parasitism. Disease and attacks by predators were responsible for no measurable portion of webworm destruction.

The usefulness of the primary parasites was very seriously hindered by the numbers of secondary parasites, that for two seasons destroyed about half of the former. It seems probable that the increase in number of webworms from 1934 to 1935 was in large measure due to the destruction of the primary parasites.

It is certain that the more important secondary parasites of Hyphantria hibernate within the cocoons of the primary parasites. These host cocoons are found in the Hyphantria webs during winter and early spring. The rains of April and May largely destroy the webs, but the tough cocoons of Hyposoter and Meteorus could afford ample protection to the secondary parasites even after being beaten to the ground. An interesting point in biological control might be brought out in this connection. Mechanical destruction of Hyphantria webs in late October and November would destroy the majority of secondary parasites without harming the two most important primary parasites, Meteorus and Hyposoter, with hibernate elsewhere as adults.

The most numerous secondary parasites were in order of importance, Catolaccus aeneoviridis Gir. and Dibrachys cavus Walk. A tertiary parasite, Tetrastichus doteni Crawford, was frequently reared from the two species of secondary parasite just mentioned.

CONCLUSIONS

The data assembled in this study seem to justify the drawing of the following conclusions:-

1. The fall webworm in Colorado is one of the several forms of a single widespread nearctic species, Hyphantria cunea Drury.

2. In Colorado, the fall webworm is single-brooded. Emergence begins in mid-June. Pupation occurs throughout the month of September.

3. An average of three hundred and fifty-six eggs are laid by a female Hyphantria moth, of which four percent may be infertile. Egg parasitism was of negligible importance during the years 1934 and 1935.

4. Hyphantria larvae under field conditions pass through at least eight stadia before pupating, and in each stadium are subject to attack by a variety of hymenopterous and dipterous parasites.

5. In 1935, by conservative estimate, at least eighty percent of the fall webworms hatching, lived to maturity and probably pupated successfully.

6. Insect parasites were the only control factors of real significance in the Fort Collins area, and of these, Meteorus acronyctae Mues. and Hyposoter pilosulus Prov. were by far the most important.

7. Less than ten percent of the deaths of webworm

larvae during the 1935 season can be attributed to the activities of parasites.

8. The ineffectiveness of the primary parasites is due to the abundance of secondary parasites.

9. The variety of species of secondary parasites and their relative abundance, together with the not infrequent appearance of the tertiary parasites may indicate a fairly stable or slowly growing webworm population over a period of years.

10. With a secondary parasitism of forty-eight percent in 1934, there was a noticeable increase in the webworm population the next year. Therefore, with a secondary parasitism of sixty percent in 1935, a further increase in webworm population in probable in 1936.

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APPENDIX

The Known Tachinid Parasites of *Hyphantria cunea*

1. *Achaetoneura aletia* Riley
2. *Achaetoneura frenchii* Will.
3. *Anetia hyphantriae* Tothill
4. *Bombyliomyia abrupta* Wied.
5. *Compsilura concinnata* Meig.
6. *Ernestia ampelus* Walk.
7. *Ernestia johnsoni* Tothill
8. *Hyphantrophaga hyphantriae* Town.
9. *Lydella hyphantriae* Tothill
10. *Masicera entfitchiae* Town.
11. *Nemoraea hyphantriae* Town.
12. *Nemoraea nigricornis* Town.
13. *Panzeria radicum* Fabr.
14. *Phorocera claripennis* Macq.

*15. *Phorocera floridensis* Town.

16. *Varichoeta aldrichi* Town.
17. *Winthemia* sp.
18. *Zenillia blanda* O.S.
19. *Zenillia blanda virilis* A. & W.
20. *Zenillia protuberans* A. & W.

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* All parasite names preceded by an asterisk in these lists are those of species here recorded for the first time from *Hyphantria cunea*.

The Known Hymenopterous Parasites of H. cunea

Primary

Ichneumonoidea

Braconidae

1. Rogas hyphantriae Gahan
2. Apanteles diacrisiae Gahan
3. " hyphantriae Riley
4. " lacteicolor Vier.
5. Perilitus communis
*6. Meteorus acronyctae Mues.
7. " bakeri C. & D.
8. " hyphantriae Riley
9. " versicolor Wesmael

Ichneumonidae

10. Amblyteles brevicinctor Say
11. " pullatus Cress.
12. Ephialtes conquisitor Say
13. Eremotylus glabratus Say
14. Labrorychus sp.
15. Therion morio Fabricius
16. " sassacus Vier.
17. Casinaria orgyiae How.
18. Neonortonia major Cress.
19. Hyposoter fugitivus Say
*20. " " pacificus Cush.
21. " pallipes Prov.

22. Hyposoter pilosulus Prov.

23. Eulimneria valida Cress.

Proctotrupoidea

Scelionidae

24. Telenomus bifidus Riley

Chalcidoidea

Tetrastichidae

25. Syntomosphyrum esurus Riley

Elachertidae

26. Elachertus hyphantriae Crawford

27. " marylandicus Gir.

28. Euplectrus sp.

Trichogrammidae

*29. Trichogramma minuta Riley

30. " pretiosa Riley

Secondary

Ichneumonoidea

Ichneumonidae

1. Hemiteles tenellus Say

Hosts:- Meteorus hyphantriae Riley

" acronyctae Mues.

Hyposoter pilosulus Prov.

2. and 3. Hemiteles spp. (two species not tenellus) Riley (377).

Hosts:- Meteorus hyphantriae Riley

Apanteles hyphantriae Riley

*4. Gelis utahensis Strick.

Hosts:- Hyposoter pilosulus Prov.

Chalcidoidea

Perilampidae

5. Perilampus hyalinus Say

Hosts:- Hyposoter fugitivus Say

" pilosulus Prov.

Chalcididae

6. Pansteron sp.

Hosts:- Apanteles hyphantriae Riley

7. Spilochalcis sp.

Hosts:- Meteorus hyphantriae Riley

Eupelmidae

8. Eupelmus sp.

Hosts:- Apanteles hyphantriae Riley

Meteorus hyphantriae Riley

Pteromalidae

9. Dibrachys boucheanus Ratz.

Hosts:- Eulimneria valida Cress.

Hyposoter fugitivus Say

Ephialtes conquisitor Say

Meteorus hyphantriae Riley

*10. Dibrachys cavus Walker

Hosts:- Meteorus acronyctae Mues.

Hyposoter pilosulus Prov.

11. *Habrocytus* sp.

Hosts:- *Rogas* Sp.

*12. *Hypopteromalus percursor* Gir.

Hosts:- *Meteorus acronyctae* Mues.

Hyposoter pilosulus Prov.

*13. *Hypopteromalus* sp.

Hosts:- *Hyposoter pilosulus* Prov.

14. and 15. *Pteromalus* spp. (two unidentified species.) See Riley (377).

Hosts:- *Apanteles hyphantriae* Riley

Meteorus hyphantriae Riley

Hyposoter pallipes Prov.

*16. *Catolaccus aeneoviridis* Gir.

Hosts:- *Meteorus acronyctae* Mues.

Hyposoter pilosulus Prov.

Eulophidae

17. *Cirrospilus* sp.

Hosts:- *Apanteles hyphantriae* Riley

18. *Elasmus atratus* How.

Hosts:- *Apanteles hyphantriae* Riley

Hyposoter pallipes Prov.

Tertiary

Chalcidoidea

Tetrastichidae

*1. Tetrastichus doteni Crawford

Hosts:- Dibrachys cavus Walker

Catolaccus aeneoviridis Gir.

The above being reared from both

Hyposoter pilosulus Prov.

and Meteorus acronyctae Mues.

ABSTRACT OF THESIS

Ralph B. Swain

THE PROBLEM

The object of this study was to find what biological control factors were operating against the increase of the population of the fall webworm, *Hyphantria cunea*, Drury, in Colorado, and whether or not these control factors were effective.

The problem had to be attacked from several different angles. Since there seemed to be some doubt as to the identity of the webworm itself, an investigation of the taxonomic status had to be made. A thorough knowledge of the life history of *Hyphantria* was necessary in order to guage the effects of the control factors. This called for field and laboratory studies of the host species. The control factors had to be first discovered by observation in the field and by rearing experiments. The parasites had then to be determined to species, and their effect upon the host calculated by means of actual counts of populations.

METHOD OF OBTAINING DATA

The investigation of the taxonomic status of the fall webworm required that the entire literature on the species be searched. In addition, the opinions of several eminent lepidopterists were asked. Webworm material from other parts of the United States was acquired and a comparison of genitalia made.

The knowledge of the webworm life history was built up through periodic observations in the field, and through rearings at the insectary. Captured females were allowed to lay eggs in the laboratory. From these eggs larvae were reared to maturity in individual cages. The head widths of the different instars and the stadia lengths were noted.

Field observations showed the major control factors in the area studied to be hymenopterous parasites. Every species of parasite collected was determined by a specialist at the United States National Museum. Estimates of the percentage parasitism of each species of parasite, primary, secondary, and tertiary were made by actual count.

COMPILATION OF DATA

The data collected during this study were in the form of field notes and daily observations, including measurements taken in the insectary. Dyer's Law was applied to the Hyphantria head width data as a check upon the number of larval stadia. Measurements and the data on webworm stadia lengths were tabulated. A graphic picture of the life cycle of the webworm was obtained by plotting population data against time.

ANALYSIS OF DATA

Special methods of analysis were not employed. The effect of control factors was judged by population counts.

SUMMARY

The moth of the fall webworm emerges at Fort Collins from mid-June to mid-July and deposits an average of three hundred and fifty-six eggs in one cluster, generally on the undersides of the terminal leaves of choke cherry or cottonwood. At least four percent of the eggs do not hatch because of infertility. A negligible fraction may be destroyed by the egg parasite Trichogramma minuta Riley. The larvae from the second stadium to the last are subject to the attacks of some six species of ichneumonid and two of tachinid parasites, of which, the ichneumons Meteorus acronyctae and Hyposoter pilosulus are the most important. The parasites destroy somewhat less than ten percent of the webworms hatching, and are themselves heavily preyed upon by a series of secondary parasites that are killing considerably above fifty percent of them at the present time. The primary parasites are aided to a very small degree by the activities of a tertiary parasite. Disease and predators of various kinds appear to play no great part in control. The large number of secondary and tertiary parasites probably indicates a stable or slowly growing webworm population over a considerable period of years. The depletion of the primary parasites by the secondary parasites may be responsible for the very considerable increase in web-

worms from 1934 to 1935. Given climatic conditions this winter comparable to those of the previous two or three, a further increase in webworm may reasonably be expected.