THE LIFE HISTORY AND POPULATION DYNAMICS OF THE VARIABLE OAKLEAF CATERPILLAR, *HETEROCAMPA MANTEO* (DRLDY.), IN MICHIGAN

By

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Abstract

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The life history and population dynamics of the variable oakleaf caterpillar Heterocampa manteo (Doubleday) were investigated in mixed oak forests of the Manistee National Forest of west central lower Michigan. Sampling techniques were designed to estimate prepupal densities in five permanent research plots. Overwintering populations of H. manteo showed little mortality, but each season ca. 50% of the prepupal population remained in a prolonged diapause lasting two years or longer.

Development times for prepupae and pupae were determined and adult flight activity monitored over two years. The fecundity potential per female was ca. 400 eggs, but parasitism levels by the egg parasitoids Telenomus sp. and Trichogramma sp. accounted for ca. 85% mortality in 1974 and 33% mortality in 1975. The larval instars were identified and the developmental times and foliage consumption of each instar determined. Each larva consumed ca. 334 cm^2 of oak foliage, but larvae parasitized by Diradops bethunei (Cresson) consumed ca. 60% less foliage. A method to predict defoliation based on relative density of early instars was devised.

Seven parasitoid species were found to attack larvae of H. manteo. Total larval parasitism in 1974 was ca. 84%, but declined to 16% in 1975. This decline was attributed in part

to the poor synchronization of many of the parasitoids to the population of H. manteo which remained 2 years or longer in the prepupal stage. Predators of H. manteo were determined and a larval defense secretion containing formic acid noted.

A laboratory rearing technique using oak foliage as a nutrient source was developed for H. manteo. The effect of temperature, photoperiod, density, and soil moisture on diapause, larval coloration, developmental times, and mortality was also investigated.

Acknowledgements

This study was made possible by the trust and foresight of the taxpayers of the United States and Canada. It is the millions of ordinary citizens, who through their tax dollars have invested in education, that merit my gratitude. I would hope that in some manner this dissertation and future endeavors will repay that trust.

Every graduate student is indebted to his major professor for long hours of guidance, professional support and a genuine concern for his well being. Dr. William E. Wallner manifested all these qualities and more. He was not simply a major professor, but more importantly, a personal friend.

To my committee members, Drs. Fred Stehr, Roland Fischer, John Hart and Wayne Myers, I am grateful for assistance in organizing a meaningful graduate program, hours of research discussions, technical expertise, and editorial assistance with this dissertation. I am indebted to all members of the Entomology Department: faculty, fellow graduate students, clerical and technical staff. Dr. James Bath has created a department providing graduate students with the finances, facilities, and above all the opportunities to expand one's potential to its limit, both professionally and personally.

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INTRODUCTION

In 1973, 20,000 to 40,000 acres of mixed oak forests of the Manistee National Forest, in the west central area of Michigan's lower peninsula, were totally defoliated by the variable oakleaf caterpillar, Heterocampa manteo (Doubleday). This research project was developed in response to that large defoliation. Since initial reported outbreaks in the late 1800's (Hooker, 1908), this insect has continued to cause scattered defoliations throughout the eastern and central United States. Between 1955-75, 18 states reported defoliations in the Cooperative Economic Insect Reports. Major infestations of over 1,000,000 acres have occurred in such diverse locations as Missouri (Kearby, 1975a), Minnesota (Wetzel, 1972), Arkansas (Anonymous, 1971) and Virginia (Anonymous, 1958).

Despite these massive infestations the insect is considered a minor forest pest. Defoliations occur late in the growing season; consequently, 2 to 3 years of consecutive defoliation are required before significant tree mortality can occur. Infestations are rarely consecutive and the host trees are generally poor quality oaks, although a wide variety of trees are subject to attack (Wilson, 1971). Defoliation does, however, reduce the vigor of trees and increases susceptibility to attack by secondary pests (Kulman, 1971). Evidence is also mounting that defoliation-weakened trees are more susceptible to infection by the root rot fungus, Armillaria mellea (Vohl.) Quel., and that the ultimate damage to

a stand from defoliation may be more serious than is immediately apparent (Houston and Kuntz, 1964; Parker and Houston, 1971). With the recent introduction of the gypsy moth, Porthetria dispar L., into Michigan, the possibility now exists that oak trees may be defoliated twice in one growing season; an early season defoliation caused by P. dispar and a late season defoliation of second flush leaves caused by the variable oakleaf caterpillar. If such a double defoliation does occur, tree mortality may be extensive. Large acreages of forest lands are aesthetically damaged and larvae represent a nuisance to homeowners and recreational users of oak forests (Millers and Erickson, 1970). In addition to aesthetic damage Kearby (1975a) has reported that larvae and prepupae secrete a formic acid solution which causes skin lesions.

The variable oakleaf caterpillar is native to North America. It has been recorded from nearly all states and Canadian provinces east of a line drawn from western Ontario through eastern Texas. It belongs to the family Notodontidae, and was first described by Doubleday (1841). Packard (1895) provided a bibliography of early taxonomic synonymy and descriptions of the egg, larval, pupal, and adult stages. Wilson (1971), based on early data, published a general description of the life history and natural controlling agents. A brief synopsis of the current information on the insect's biology, based primarily on Wilson's (1971) description, is presented. This is intended to provide an overview of the life history, predators and parasitoids of the insect as known before this study was initiated.

There is one generation per year in the northern

part of the variable oakleaf caterpillar's range. In the area south of a line extending from Virginia to Missouri, two generations are common (Wilson, 1971). The insect overwinters as prepupae in silken cells constructed in the leaf litter and soil. Pupation normally occurs the following spring although some prepupae have been reported to remain in the soil for a year or more before pupation. Adult moths in the northern range begin to emerge near the end of May or early June and lay their eggs singly on the leaves of the host (Wilson, 1971). Each female may lay as many as 500 eggs which hatch in 7 to 10 days. The first instars skeletonize the lower surface of the leaves, but subsequent instars consume the entire foliage between the major veins. About mid-August the larvae cease feeding, drop to the ground and spin silken cells in which they overwinter.

In the south where two generations per year occur, the moths emerge about mid-April. Eggs are laid and larvae feed during May to early July. The larvae then drop to the soil and pupate. Adult moths emerge and lay their eggs in late July, with feeding of newly hatched larvae completed by late September or early October. The fall generation then overwinters as prepupae; with pupation occurring in April of the following year.

The information concerning the predators and parasitoids of H. manteo and their impact upon population control was meager. Wilson (1971) stated, "Several species of insects of the families Tachinidae, Ichneumonidae, and Braconidae have been reared from the closely related saddled prominent and probably attack the variable oakleaf caterpillar as

well." No information on parasitoids of H. manteo had been published. Hooker (1908) reported that in Texas the predatory ground beetles Calosoma scrutator Fab. and Calosoma calidum Fab. were found on oak trees with larvae of H. manteo in their mandibles.

Despite the large acreages defoliated by H. manteo and its aesthetic impact on homeowners and recreational users, there existed no substantive study of the life history and population dynamics of this insect. The principal objective of this study was to develop a comprehensive understanding of the life history and population dynamics of H. manteo in Michigan. Specific efforts were made to monitor population levels, parasitism rates, and the effect of the environment upon survival and development of the insect's life stages. Attempts were also made to formulate methods for predicting defoliation.

Research Area

In the summer of 1973, 5 permanent research plots were established on federal land in the Manistee National Forest. Each plot was 4 hectares in size with trees consisting predominantly of northern red oak, Quercus borealis var. maxima Mich., and white oak, Quercus alba L. In addition, some red maple, Acer rubrum L., beech, Fagus grandifolia Ehrh., eastern white pine, Pinus strobus L., and sassafras, Sassifras albidum (Nutt.), were present in all plots. The plots were selected on a north-south transect within the Manistee National Forest (Fig. 1). This transect also provided an opportunity to study populations of H. manteo at

various densities. All research sites had been severely defoliated by the redhumped oakworm, Symmerista canicosta Franclemont, during 1970, '71, and '72 (Robertson et al. 1972; Millers and Wallner, 1975).

The most southerly plot, designated Newaygo, was 5 km north of Newaygo, Michigan in Newaygo County, Everett twp., T13N, R12W., Sec. 30. Trees within this plot consisted of pole-sized red and white oaks approximately 25 cm in dbh. The Big Star Lake plot was considered the epicenter of the 1973 defoliation with 100% of the foliage consumed. This plot was approximately 56 km north of the Newaygo plot, in Lake County, Lake twp., T17N., R14W., Sec. 33. Trees consisted of red and white oak approximately 30 cm in dbh. Two plots were located in the vicinity of Branch, Michigan, Lake County, Sweetwater twp., T18N., R14W., Sec. 4 and 5. These plots were selected in close proximity to each other (1.2 km) to investigate the effects of tree age on population dynamics of H. manteo. The plot, designated Branch Mature, consisted of mature oaks with an average dbh of 40 cm. The Branch Pole plot was comprised of pole-sized oaks with an average dbh of 25 cm. These 2 plots were completely defoliated by larvae of H. manteo during August, 1973. The fifth plot was located 1 km north of Dublin, Michigan. The precise location was Manistee County, Norman twp., T21N., R14W., Sec. 36. This area consisted of red and white oaks approximately 25 cm in dbh which had been severely defoliated by S. canicosta Frclmt. during 1971 and 1972.

All five plots were situated on marginal lands possessing poor, sandy soil, low in fertility and moisture hold-

Fig. 1. Location of research plots for the study of *H. manteo* populations in Michigan 1973-76.

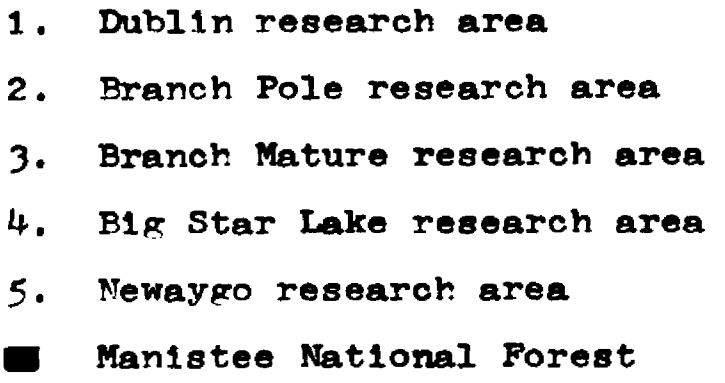

FIG. 1.

ing capacity. The soils of the region have been classified as Rubicon-Grayling (Veatch, 1953). The area was previously covered with white pines which were harvested in the late 1800's. The organic layer of soil in all 5 plots never exceeded 13 cm; below which mineral sand was present to an unknown depth. A soil sample from Branch Pole indicated that an 8 cm diameter core of soil removed to a depth of 20 cm contained 75% sand, 15% clay and 10% loam. Perhaps, the greatest value of the oak trees in this region is their soil conservation preperties.

Method for Estimation of Prepupal Populations

The sampling techniques used to estimate insect populations have been reviewed by Morris (1955) and Southwood (1966). In this study an estimate of absolute population (no./unit area) was most suitable for long term population estimates. The most easily sampled life stage is the prepupa of H. manteo. Prepupae are defined as those larvae which have entered the soil-litter to overwinter. They differ physiologically from larvae in that they have ceased feeding, have completely evacuated the digestive tract, and exhibit a photo-negative response. This stage is most suited for sampling because the duration of the prepupal stage is considerably longer than all other life stages combined. Prepupae remain stationary once they have entered the litter, so samples can be taken during the late fall and early spring months when time demands are minimal. Ideally, the sampling procedure would satisfy the following criteria:

1) allow for a comparison of populations between plots.
2) indicate spatial distribution of prepupae.
3) allow for a comparison of populations through time.
4) indicate areas of high or low density within plots by mapping the number of prepupae recovered per sample.
5) provide living specimens to be used in further research.

Prepupal samples were based on a quarter of a square meter (50 cm x 50 cm) of soil and litter removed to a depth of 10 cm. Grimble and Newell (1972a) had used a similar procedure to estimate pupal populations of Heterocampa guttivitta (Walker).

In each plot a systematic sample grid composed of 20 subplots was established. Each subplot was 36 m from adjacent subsamples (Fig. 2). In October of 1973 soil litter samples from each subplot were removed. The sample unit size was standardized using a 50 cm x 50 cm aluminum frame. A straight-bladed shovel was used to cut along the inner margin of the frame and remove the soil and litter. Each sample was placed into a 30 cm x 76 cm x 20 cm polyethylene bag and labelled according to plot, grid location, and sample date. Prepupae which lay on the sample perimeter and were severed by the shovel were included within the sample. In a similar manner 3 additional sets of samples were taken 1 meter from the original grid location. These samples were timed to measure possible winter mortality, predation of prepupae in the spring, and proportion of the population which remained in the soil-litter for a year or more. In the autumn of 1974

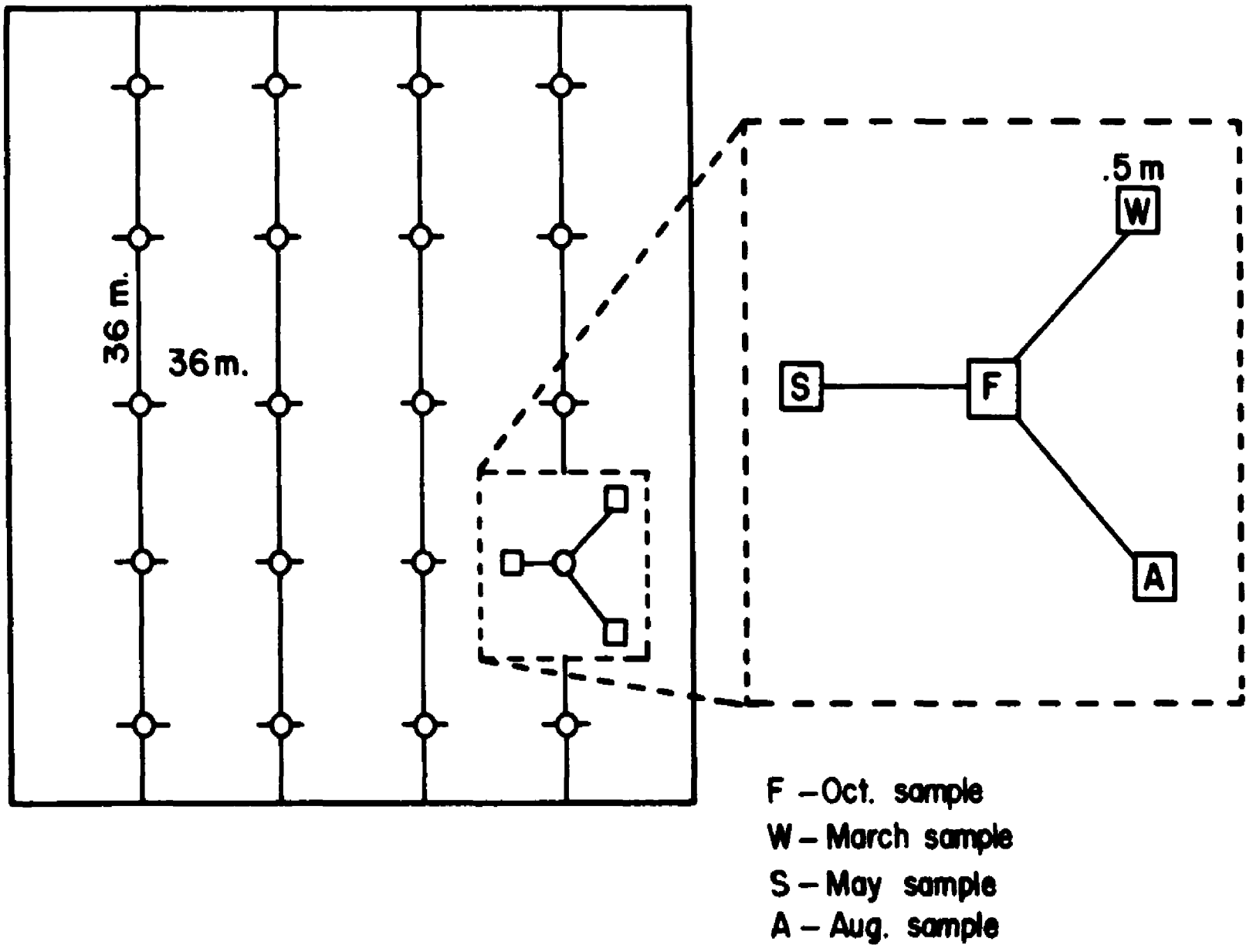

Fig. 2. Diagram of sampling design used to estimate prepupal densities of H. manteo, Michigan, 1973-6.

and '75 the grid was shifted 5 meters to the north in all plots to minimize the possible effect of litter removal on prepupae entering the soil at the cessation of feeding in 1974 and 1975.

Samples were refrigerated at 4.4° C until soil and litter were sieved. The samples were broken by hand into small pieces and sieved through .64 cm wire mesh screening. Prepupae were found in curled repose similar to that of white grubs and were too large to pass through the mesh. They were readily apparent in the sieve frame because their red (Fig. 3) and green (Fig. 4) colors contrasted markedly with the dark soil and litter. By examining soil which had passed through the sieve it was estimated that recovery exceeded 95%.

Prepupae were segregated as to plot and recorded according to grid location. The color of prepupae; whether green, pink, or red was also recorded. Prepupae parasitized by Diradops bethunei (Cresson) were also determined for each sample by examining prepupal body and head capsule size (Fig. 3) (Surgeoner and Wallner, 1975).

Prepupal Densities and Distribution

The results of prepupal samples are presented in Tables 1-5. The sampling technique provided a measure of population densities with a standard error approximately 20% of the mean. By plotting the variance vs. the mean (Fig. 5) for all 5 plots it was apparent that prepupae were contagiously distributed ($S^2 > \bar{X}$) at high densities, but that at low densities the population approached a Poisson distri-

bution ($S^2 = \bar{X}$).

The sample distributions for each date were tested using a Kolmogorov-Smirnov test. At the lower densities (ca 1.5 prepupae per .25 m^2), the distributions were Poisson ($p < .05$); at densities greater than 2 prepupae .25 m^2 the distributions were determined to be negative binomial ($p < .05$). There was no clear indication why prepupae were clustered within certain samples. In areas of high prepupal concentration, additional samples were removed 1 meter adjacent to previous samples. The variability between these samples was extremely high which indicated clustering resulted from micro environmental factors. Grimble and Newell (1972a) found no clear indications of preferred pupation niches for H. guttivitta.

In a long term study of this nature, information concerning whether the population was increasing or decreasing through time was necessary. Prepupal samples present an excellent indicator of population change. The index of each overwintering population to that of the previous year is presented in Table 6. The populations in all study plots have continued to decline since the defoliations of 1973. The overwintering population in 1975 was approximately 33% of the 1973 population.

Wilcoxon's matched-pairs signed ranks test showed that populations at Big Star Lake were significantly higher ($p < .01$) than all other plots. This was expected since the area was considered the epicenter of defoliation. Prepupal densities for any sample date at Branch Pole were not signi-

FIG. 3. Red color phase of Heterocampa manteo (Doubleday) (Mag. 2.5x)
A) Parasitized by Diradops bethunei (Cresson)
B) Normal prepupa

FIG. 4. Green color phase of H. manteo prepupa showing traces of red coloration (Mag. 2.5x)

Table 1. Prepupal densities of *H. manteo*, Newaygo, Michigan, 1973-75.

	Mean/.25m^2	Sd.	Var.	S.E.	S.E. % Mean
Oct 11/73	2.55	2.63	6.92	.59	22.3%
Mar 20/74	2.75	3.02	7.56	.67	24.5%
May 17/74	2.50	1.96	3.84	.43	17.6%
Sept 4/74	1.60	1.98	3.92	.44	27.6%
Oct 27/74	1.70	2.03	4.12	.45	28.3%
Apr 15/75	1160	2.56	6.55	.57	35.8%
May 11/75	1.85	2.01	4.04	.44	24.3%
Aug 6/75	1.05	1.00	1.00	.22	21.3%
Oct 21/75	.50	.69	.48	.15	30.1%

Table 2. Prepupal densities of *H. manteo*, Big Star Lake, Michigan, 1973-76.

	Mean/.25m^2	Sd.	Var.	S.E.	S.E. % Mean
Oct 12/73	7.20	5.13	26.3	1.2	15.9%
Mar 20/74	9.35	7.21	51.9	1.6	17.2%
May 17/74	8.35	3.80	14.4	.85	10.3%
Aug 21/74	2.75	1.83	3.7	.40	14.9%
Oct 27/74	5.20	2.98	15.8	.89	17.1%
Apr 15/75	6.85	4.76	22.7	1.06	15.5%
May 10/75	4.80	3.04	9.2	.68	14.2%
Aug 6/75	2.55	2.74	7.5	.61	24.0%
Oct 21/75	3.25	4.10	16.8	.92	28.3%
Apr 8.76	2.35	2.10	4.45	.47	20.0%

Table 3. Prepupal densities of H. manteo Branch Pole, Branch, Michigan, 1973-76.

	Mean/.25m^2	Sd.	Var.	S.E.	S.E. % Mean
Oct 20/73	3.65	2.76	7.61	.62	16.9%
Apr 8/74	2.85	2.03	4.12	.45	15.9%
May 24/74	2.25	2.24	5.01	.50	22.2%
Aug 23/74	1.40	1.50	2.25	.33	23.9%
Oct 27/74	1.90	1.59	2.53	.36	18.7%
May 1/75	1.85	1.39	1.93	.31	16.8%
June 16/75	2.25	2.02	4.08	.45	20.0%
July 20/75	1.35	1.23	1.51	.27	20.3%
Oct 20/75	1.20	1.40	1.96	.31	26.0%
Apr 8/76	1.05	.94	.89	.21	20.0%

Table 4. Prepupal densities of H. manteo Branch Mature, Branch, Michigan, 1973-76.

	Mean/.25m^2	Sd.	Var.	S.E.	S.E. % Mean
Oct 20/73	3.40	3.22	10.37	.72	21.1%
Apr 8/74	3.20	2.19	4.80	.49	15.3%
May 24/74	3.15	2.56	6.55	.57	18.2%
Sept 4/74	1.55	1.39	1.93	.31	20.0%
Oct 27/74	2.25	2.29	5.24	.51	22.8%
May 1/75	1.70	1.53	2.34	.34	20.1%
July 20/75	1.20	1.31	1.72	.29	24.4%
Oct 20/75	1.20	1.24	1.54	.28	23.1%
Apr 8/76	1.55	1.84	3.41	.41	26.5%

Table 5. Prepupal densities of H. manteo, Dublin, Michigan, 1973-75.

	Mean/.25m^2	Sd.	Var.	S.E.	S.E. % Mean
Oct 12/73	2.70	2.68	7.18	.60	22.1%
Apr 8/74	1.90	2.34	5.47	.52	27.5%
May 24/74	1.40	1.64	2.69	.37	26.1%
Sept 4/74	.85	1.04	1.08	.23	27.3%
Oct 27/74	.75	1.16	1.35	.26	34.5%
May 1/75	1.45	1.90	3.61	.42	29.3%
Aug 7/75	.40	.75	.56	.17	41.9%
Oct 20/75	.65	.99	.98	.22	34.0%

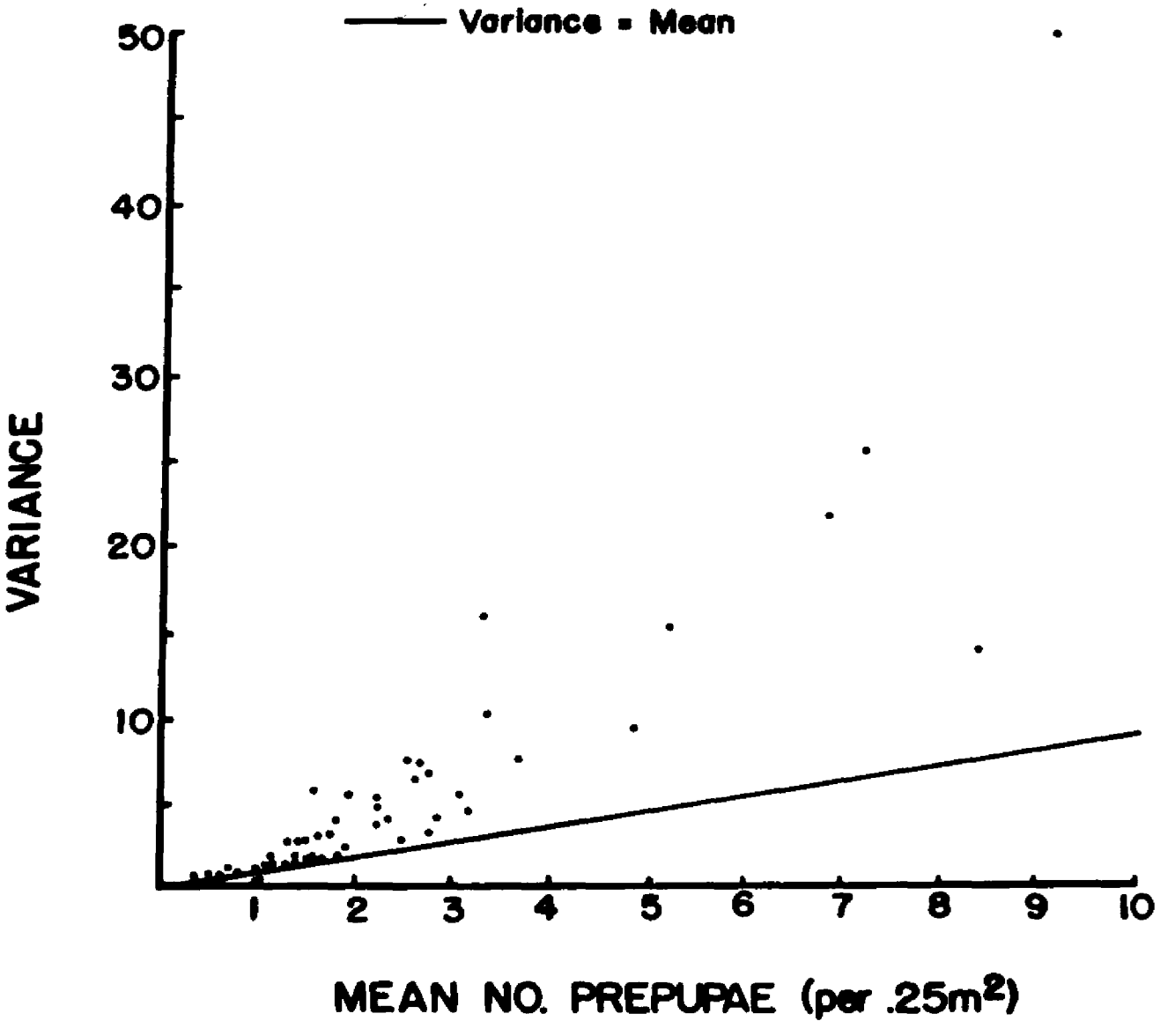

FIG. 5 Variance vs. mean of prepupal samples, Michigan, 1973-76.

Table 6. Generation index of H. manteo prepupal populations, Michigan, 1973-75.

	$\bar{x}$ prepupae/.25m^2			Generation Index		
Plot	Oct 73	Oct 74	Oct 75	73-74	74-75	73-75
Newaygo	2.55	1.70	.50	.66	.29	.20
Big Star	7.20	5.20	3.25	.72	.63	.45
Branch Pole	3.65	1.90	1.20	.52	.63	.39
Branch Mature	3.40	2.25	1.20	.66	.53	.35
Dublin	2.70	.75	.65	.28	.86	.24

ficantly different from those of Branch Mature which indicated tree age did not affect prepupal populations.

During this study prepupal densities did not provide a reliable method for predicting defoliation. Despite an overwintering prepupal population at Big Star Lake of approximately 8 prepupae/.25m^2 in 1973, there was little evidence of defoliation in 1974. This was explained in part by the large number of prepupae which remained in prolonged diapause and by extremely high levels of egg parasitism in 1974. Grimble and Newell (1972a) similarly, reported pupal densities of H. guttivitta were poorly correlated with subsequent defoliation. Prepupal densities do, however, indicate where the potential for defoliation existed.

Soil Samples as a Detection Survey

Detection surveys measure the presence or absence of an insect population in a particular area. Ideally, the sample method should detect low density populations and yet require little time, training, man-power or equipment. The use of 5, .25m^2 samples taken along a straight line with points spaced 36 meters apart provides a survey method to detect prepupal populations of H. manteo. Experience has shown that a single person with a shovel, .25m^2 frame and seive (.64 cm mesh) can complete such a survey for an area in less than 40 minutes.

The accuracy of this survey technique was based on data collected estimating prepupal populations using 20, .25m^2 samples. At the lowest densities found in the three-year study (ca. .5 prepupae/.25m^2) 12 of 20 samples contained

zero prepupae (Fig. 6). The probability of detecting at least 1 prepupa in 5 samples at such densities was 1 - $(\frac{12}{20} \times \frac{11}{19} \times \frac{10}{18} \times \frac{9}{17} \times \frac{8}{16}) = .95$ or 95%. At densities ca. 1 prepupae/.25m^2, in the plot with the highest proportion of zeros, 9 of the 20 samples contained zero prepupae. The probability of detecting at least 1 prepupa in 5 samples at such densities was 1 - $(\frac{9}{20} \times \frac{8}{19} \times \frac{7}{18} \times \frac{6}{17} \times \frac{5}{16}) = .99$ or 99%. At densities above 3 prepupae per .25m^2 there was never an instance when 5 or more samples contained zero prepupae. Detection surveys as described can therefore be used to locate populations of prepupae at densities of .5 prepupae/.25m^2 and above.

This type of survey can be carried out in mixed oak forests from Sept. to Nov. and Apr. to July in a northern area such as Michigan. When populations are detected, a researcher may expand the number of samples to 20 for an estimate of prepupal populations.

A prediction of defoliation cannot be based on prepupal estimates. Actual prediction must be based on early instar populations (see prediction of defoliation). This type of sampling scheme allows the researcher to identify areas with the highest prepupal densities and therefore the highest probability for defoliation. These areas may then be sampled in August to estimate early instar densities for possible defoliation.

A series of detection surveys was conducted in mixed oak forests throughout the state. Samples were taken during June, 1975, in the vicinity of Ellis Lake, Ludington, Filer City, Cadillac, Muskegon, Greenville and Brethren, Michigan.

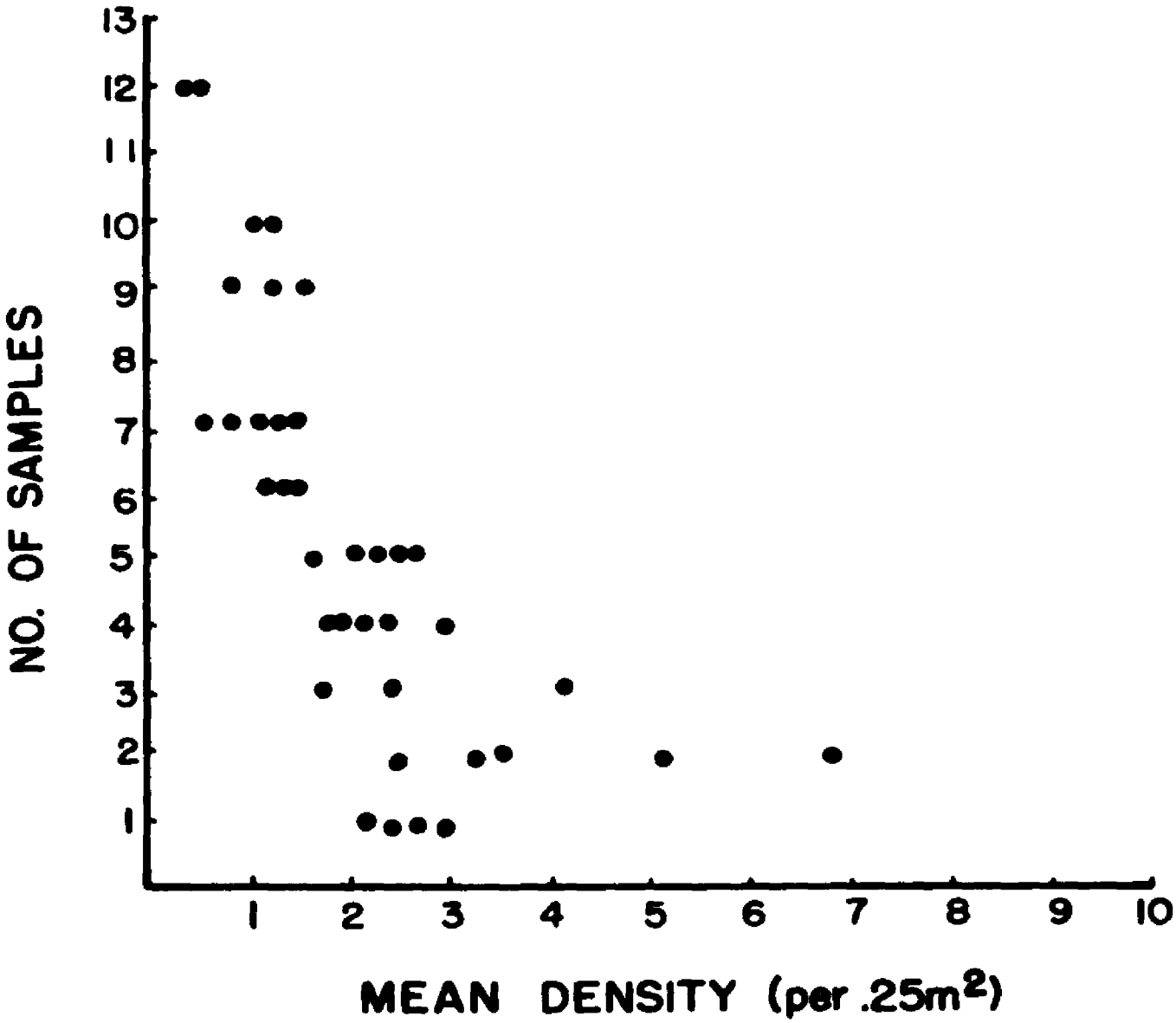

FIG. 6 Number of samples containing zero prepupae per 20 samples vs. mean density of prepupae.

Only at Brethren, Michigan, which was nearest to the research plots, were prepupae detected (.4 prepupae/.25m^2).

Coloration of Larvae and Prepupae

The variable oakleaf caterpillar was so named because of the tremendous variation of colors and pattern found in the larvae and prepupae. Larvae and prepupae vary from solid red (Fig. 3) to nearly complete green (Fig. 4). This color and pattern variability has been reported from all areas in which H. manteo is distributed (Wilson, 1971).

Prepupae collected in Oct., 1973, varied through all color types. The prepupae in samples were categorized as red, pink or green. In the highest density plot, Big Star Lake, the red color predominated, and as density declined the percentage of red colored prepupae also declined, Table 7. By comparing the percentage of red prepupae in the fall and subsequent spring samples, it was evident that the numbers of red prepupae declined, Table 8. In April, 1976, no red prepupae were found in soil and litter samples. These declines in red prepupae were explained because individual prepupae actually change color. The red pigment gradually fades to pink and eventually to green with small traces of pink still evident (Fig. 4). All prepupae observed in the laboratory were bright green immediately before pupation. Packard (1895) based on information supplied by C.V. Riley reported that all prepupae became a uniform paris green despite the fact that several color types were placed into the soil. In feeding trials, larvae of H. manteo were capable of

changing colors. Green larvae with a red band on the dorsum, the thorax and first abdominal segments (Fig. 7) changed to a dull, pink color (Fig. 8) when feeding ceased. The complete color change occurred within 24 hours. Klots (1967) and Dyar (1891) had previously observed dramatic color changes in the final instars of Heterocampa when feeding ceased. Klots (1967) found that fifth instars of H. pulverea (Grote and Robinson) turned a brilliant pink when feeding ceased, but that this color faded to a pale green just before pupation. The color change of H. manteo to a greyish-pink may increase prepupal survival on the forest floor since the green larvae are readily apparent against the background of fallen leaves. This advantage, if any, is considered minor since all prepupae observed burrow directly into the litter.

The possible significance and determining factors of H. manteo coloration are questionable. Since prepupae of high density populations possess the greatest red color, coloration may be density dependent (Iwao, 1968). Other possible explanations are that color is characteristic of population quality (Wellington, 1964) or that color is dependent upon diapause induction (Tauber et al., 1970), or the nutritional quality of the host (Palmer and Knight, 1924). Fuzeaw-Breasch (1972) has reviewed the factors which can induce color changes. Klots (1967) found that sibling larvae of H. pulverea show a marked dimorphism. He concluded that larval dimorphism was not linked with the rate of development, sex or any discernible adult characteristic.

Tests were conducted to determine if larval density

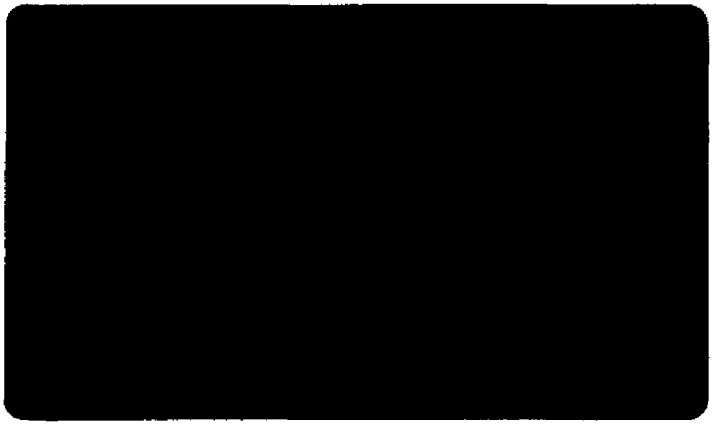

Fig. 7. Possible color pattern of H. manteo larva feeding in canopy (Mag. 1.5 x).

Fig. 8. Typical color pattern of H. manteo larva upon cessation of feeding (Mag. 2.5x).

Table 7. Prepupal color types of H. manteo as related to density, Michigan, Oct. 1974.

Location	Density/.25m^2	% Green	% Pink	% Red
Newaygo	2.55 ± 2.6	18	45	37
Big Star Lake	7.20 ± 5.1	15	22	63
Branch Mature	3.40 ± 3.2	19	29	52
Branch Pole	3.65 ± 2.7	26	25	49
Dublin	2.70 ± 2.7	26	48	26

Table 8. Seasonal color patterns of H. manteo prepupae Michigan, 1973-74.

Season	% Prepupae Green	% Prepupae Pink	% Prepupae Red	% Prepupae Red Par. 1976
Fall, 1973	20.8	33.6	45.8	0
Winter, 1974	28.6	35.0	36.2	
Spring, 1974	36.8	39.4	24.0	
Summer, 1974	55.8	37.2	6.8	
% Change Fall-Summer	+35.0	+3.6	-39	

affected the color patterns of H. manteo. Twelve larvae from a single egg mass were reared at different densities; in one instance 6 larvae were reared individually, each being fed in a single pint-sized container. The other 6 larvae were reared together within a single pint container. Both groups of larvae were maintained at 24°C with a 16-hour photoperiod. Larvae reared individually never consumed all the food provided; whereas, during the final instar, larvae reared together consistently ate all food provided such that in each 24-hour period approximately 6 hours were spent without food. There was no significant difference in color or pattern of individual or group reared larvae. This indicated that larval color was not density dependent or determined by a shortage of foliage.

I concluded from rearing over 200 larvae that color was not dependent upon photoperiod; larvae reared in complete darkness maintained the same color and pattern as siblings reared under a 16-hour photoperiod. Siblings reared at 26°C, 24°C, 20°C and 15°C did not differ significantly in color. By rearing over 200 larvae through to adults I concluded that larval or prepupal coloration was not sex-linked nor linked to any discernible adult coloration.

As previously noted the color of prepupae gradually faded from red to green as they neared pupation. A study was conducted to ascertain if field-collected green prepupae pupated significantly sooner than red prepupae. Prepupae were collected from Big Star Lake in March of 1974. They were segregated by color and placed individually into 50 ml

jars filled with soil and litter (soil moisture, 18%) and maintained at 24°C, and 16-hour photoperiod. The mean number of days required for pupation by the green prepupae was 29.2 ± 12.57 days compared to 36.8 ± 12.5 days for red prepupae. This was significantly different using Wilcoxon's matched-pairs signed ranks test ($p < .05$). The color of prepupae appeared to reflect the physiological age of the individual with green indicating a more mature condition.

This knowledge may prove valuable when prepupal samples are made in an area. If fall or early spring samples are predominantly red (Fig. 3) a researcher can assume that a major component of the prepupae are from the current year. If, however, the majority of the prepupae are green to dull pink (Fig. 4) one can assume that a majority of the prepupae are from a population which has remained in the soil a year or longer (see diapause section). For example, during the growing season of 1975, larvae of H. manteo were extremely rare at Big Star Lake, Michigan. Pyrethrum spraying of mature oak trees showed an average of less than 20 larvae per tree (see larval sampling). During late August, 1975, 3 experienced collectors spent 6 man-hours searching for larvae on the foliage and discovered only 12 individuals. However, soil samples in the fall and spring showed an average of 2.5 prepupae/.25m^2. The majority of these prepupae must have carried over from populations in 1973 and 1974. This was strongly indicated because no red prepupae were found in samples during Oct., 1975 or April 1976; whereas, in Oct., 1973, approximately 69% of the prepupae were red in color.

Defensive Secretions

Prepupae of H. manteo frequently spray a fine mist which produces an extremely pungent odor similar to that of formic acid. This secretion causes a burning sensation to cuts but none to normal skin. When tasted the substance caused a severe burning sensation to the tongue, but no lesions. In Missouri the secretions caused vesications and skin lesions to those handling variable oakleaf caterpillars (Kearby, 1975a). The reaction to collectors in Michigan was not as severe since no blistering occurred.

The opening to the gland producing the secretion is a narrow slit on the median of the ventral prothoracic segment (Fig. 9). The position of the gland is identical to that of Schizura cocinna (Abbot and Smith) described by Detwiler (1922). The gland opening is everted at the time of spray ejection (Fig. 9) which apparently allows some directional control of the spray. The secretion was observed to be expelled several centimeters. Several prepupae were dissected, which revealed that the gland producing the secretion extended posteriorly into the meso and meta-thoracic segments occupying a large volume of the thoracic cavity. The gland consists of two small anterior sacs and a single large posterior sac (Fig. 10). Detwiler (1925) had previously described a similar internal gland for several notodontid larvae.

The substance secreted was analyzed by Dr. M. Zabik, biochemist, Dept. of Entomology, Michigan State University, and was found to be comprised of formic acid and probably

some long chain fatty acids. Poulton (1886), Packard (1886), and Herrick and Detwiler (1919) have all reported formic acid secretions by larvae of Notodontidae. The other chemical compound associated with the secretion of H. manteo has been reported to be acylic ketones (Eisner et al. 1972).

When early instars were handled in the field collectors discovered that formic acid secretions were ejected by second and subsequent instars. First instar larvae were never observed to eject any fluid. A carabid adult, Pinocedera sp., was observed to approach a fifth instar. The larva sprayed the adult beetle which immediately retreated, cleaning its eyes and antennae. A similar repelling action was noted by Eisner et al. (1972) in tests conducted with Lycosoma sp. The acylic ketones of H. manteo repelled formic acid-producing ants (Eisner et al., 1972). Kearby (1975a) reported that no birds were observed to feed on larvae in Missouri; similarly, no birds were observed feeding on active larvae in the canopy in Michigan. Kearby (1975a) suggested that the lack of bird predation may be a result of these defensive secretions.

There was little predation of prepupae in the soil. This was determined by comparing overwintering populations to populations the following years. Wilcoxon's matched-pairs signed ranks tests showed no significant difference between fall populations in 1973-75 to those the following May and April ($p < .05$). Shrews, deer mice, Peromyscus minicula-tus bairdii (Hoy & Kenicott), white-footed mice, Peromyscus leucopus (Rafinesque), have been reported as predators of

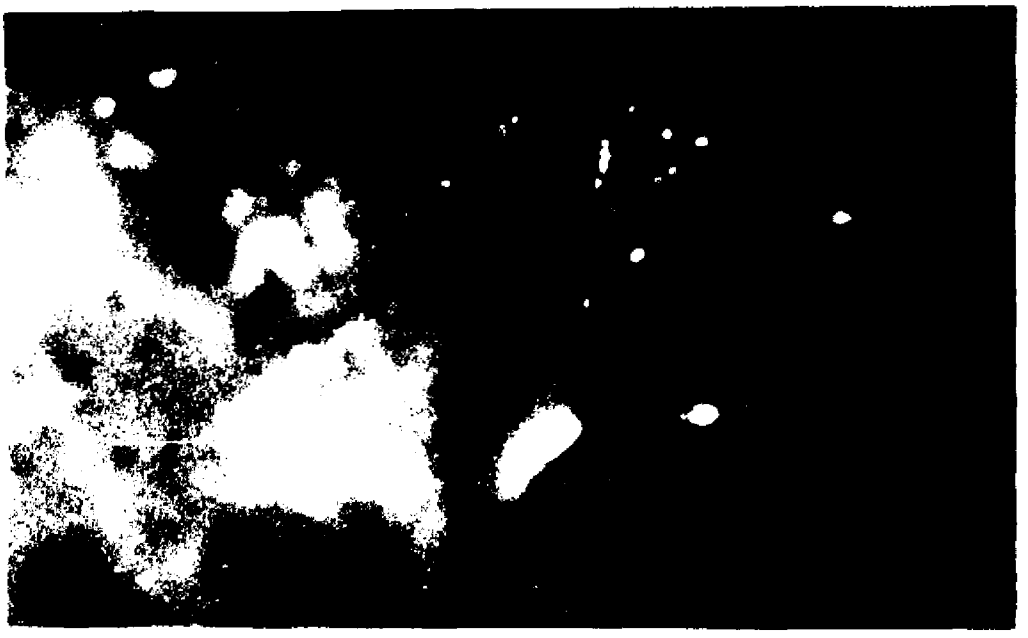

Fig. 9. Opening of defense gland of H. manteo immediately prior to formic acid ejection (Mag. 13x).

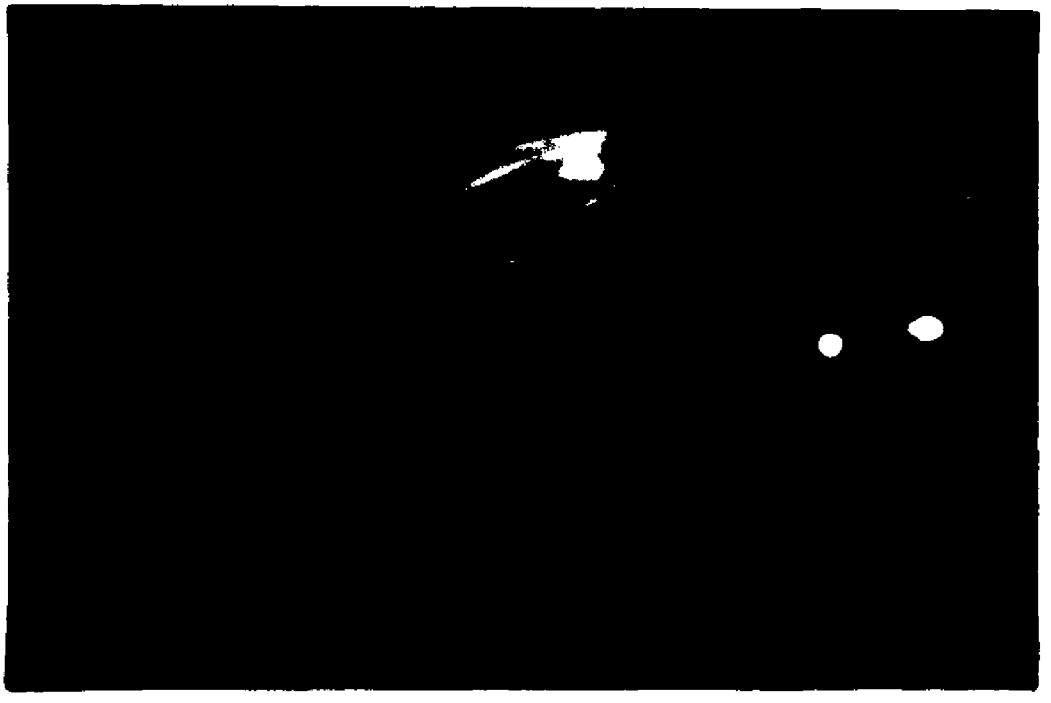

Fig. 10. Defense gland of H. manteo showing three chambers (Mag. 13x).

insect populations causing significant population mortality (Holling, 1959; Campbell, 1975). These vertebrates were present in the research plots, but apparently rarely fed on prepupae. The prepupae maintain a relatively large supply of defensive secretion. Eisner et al. (1972) discovered 10, 13, and 22 mg. of secretions in the three sacs of H. manteo fifth instars. Although overwintering prepupae do not eject any fluid, the supply of formic acid and ketones may deter predation by vertebrates which have previously attempted to consume prepupae. The red and green colors of larvae may serve to warn potential predators.

Cold Temperature Mortality Studies

In Minnesota soil samples collected in 1944 indicated an average of 6 prepupae per ft^2 under infested trees, but in 1945, no larvae of H. manteo were found in the canopy (Wetzel, 1972). In Virginia (Anonymous, 1958), where several million acres were defoliated in 1956 there was little or no adult emergence despite the fact that prepupae were abundant in the soil during 1956-57. Declines in populations of H. manteo may have resulted from predation or cold-temperature mortality of overwintering prepupae. A study was therefore conducted to determine cold-temperature tolerances of prepupae.

To assure cold-hardiness, prepupae were collected from Big Star Lake during February of 1974. Prepupae sieved from samples were stored in moist litter at 4.4°C until cold-tolerance trials were initiated. The storage period never exceeded 1 week. Prepupae removed from storage were placed

in 23 cm long, 9 mm glass tubes where they were separated by nylon screening. Six prepupae were placed in each tube which was furnished with a few drops of water at the bottom, before sealing the top and bottom with rubber plugs. The tubes containing prepupae were placed in ethylene glycol-water baths maintained at constant temperatures as described by Casagrande (1975).

Prepupae remained in the cold temperature baths for a 24-hour period at which time the tubes were removed from the baths. They were then held at 20°C for 4 hours after which mortality was assessed. Prepupae were examined under a steromicroscope and the mouthparts touched with a metal probe. If no response to the probe was noted, the prepupa was considered dead. The results of cold temperature trials are presented in Table 9.

Results indicated that under these conditions prepupae were unable to withstand temperatures below -6.8°C and that significant mortality occurred below 0°C. Prepupal samples (Table 1-5), however, indicated that there was no significant mortality during the winter months of 1973, 1974 or 1975. Wilcoxon's matched-pair signed ranks tests were used to compare the fall and spring samples for the years 1973-76. In no instance was there a significant reduction in prepupal numbers ($p < .05$). Soil temperatures were recorded during the winter of 1974-75 using a Weathervane (Model T-603-16) three-point, 31-day recording thermograph. The temperatures were monitored at the surface of the litter, at the litter-soil interface (7.6 cm deep), and within the mineral sand approxi-

Table 9. Percent mortality of H. manteo prepupae exposed to cold temperatures for a 24-hour time period.

Temperature	% Mortality	No. of Larvae Tested
-6.7°C	100	32
-5.5°C	94.1	17
-3.9°C	53.7	54
-2.2°C	29.4	17
-1.1°C	23.2	56
0°C	11.1	72

mately 30 cm in depth. The thermograph showed that temperatures at the surface remained constant at 0°C throughout the winter months and +2.2°C at the litter-soil interface where prepupae are found. The temperature in the mineral soil was approximately 1.1°C throughout the winter. There was little or no fluctuation of these temperatures from mid-November, 1974, until early April 1975, because snow cover acted to insulate diurnal fluctuations. Prepupae were never exposed to lethal temperatures during the winter of 1974-75. During the 3 winters of this study, the litter or soil was never found to be frozen. Prepupae apparently seek out a habitat in which winter temperatures do not reach lethal levels. Such a behavioral survival mechanism was termed frost avoidance (Salt, 1961). The digestive systems of prepupae were always totally evacuated, another mechanism to minimize the possibilities of mortality by freezing (Salt, 1953) or fungal and bacterial infection.

Diapause and Prepupal Development

Diapause is defined "as a state in which a reduction of growth processes or maturation occurs which is not necessarily caused by immediate environmental influence, does not depend for its continuation on unsuitable conditions, and is not easily altered by change to a more favorable condition" (Simmonds, 1948). Diapause may be of two types, either obligate or facultative (Andrewartha, 1952). Obligate diapause is defined as inherent and seems to occur independent of any normal variation in the environment. Facultative diapause

occurs as a response to the appropriate stimulus from the environment.

Prepupae of H. manteo drop from the canopy to the forest floor upon the cessation of feeding. This was confirmed by placing inverted cone traps with a basal area of .25m^2 under infested trees; large numbers of prepupae were discovered within these traps which indicates that caterpillars drop to the forest floor rather than crawl down the tree bole. Once on the forest floor the insect then burrows into the leaf litter and soil, overwinters in a silken cell approximately 3 cm in diameter. The cells are generally found at a depth of 8 cm where the humus and mineral soil interface, although some prepupae (5%) can be found within the leaf litter. The prepupae diapause within the cell throughout the winter and early spring before pupating and emerging as adults in late July.

Prepupae collected in October, 1973, were placed individually into 50 ml glass jars filled with 30 gm of field-collected litter and soil containing approximately 18% H_2O by weight. These jars were then placed in Sherer environmental chambers from 20 Oct., 1973 to 28 Dec., 1973; a period of 69 days. Consequently, prepupae were held at 4.4°C for 3 months before studies were conducted to assess the effect of temperature on prepupal development. In addition, prepupae were collected in the months of March, April and May after successfully overwintering. Prepupae collected in the spring were also placed individually into 50 ml glass jars

filled with 30 gm of field-collected litter and soil. The jars were labelled, sealed with lids and placed in Sherer environmental chambers. One chamber was controlled at 24°C with a 16-hour light and 8-hour dark photoperiod; additional chambers were maintained at 20°C, 15°C, 10°C, and 4.4°C with complete darkness.

The results of prepupal rearings are presented in Table 10. Sex of prepupae did not significantly affect developmental time ($p < .05$). There was no development of prepupae at temperatures of 10°C or lower, but development did occur at 15°C. The minimum termperature for pupation was approximately 12.5°C. Prepupae were found to remain viable for up to 7 months when stored at temperatures between 4.4°C and 10°C.

The time required for pupation showed extreme variability. This variability was explained in part because prepupae were of different physiological ages. The prepupal coloration served as an indicator of these ages (see H. manteo coloration). The intensity of diapause also explained a major component of the variability in developmental times. Tauber and Tauber (1976) stated that "diapause is largely a dynamic state, i.e. as the season progresses, diapause depth or intensity decreases, and the animal's response to diapause-maintaining factors diminish." The date on which prepupae were collected from the field was correlated with the time necessary for pupation.

The time necessary for development of prepupae col-

Table 10. Developmental times of H. manteo prepupae.

Temperature of Environmental Chamber	Mean No. Days Until Pupation	
	Female	Male
24°C	23.1 ± 11.7	23.4 ± 11.2
20°C	34.8 ± 19.2	36.8 ± 20.7
15°C	38.2 ± 17.8	39.4 ± 14.8
10°C	No pupation	
4.4°C	No pupation	

lected in the field on 8 April, 1974 is presented in Fig. 11; whereas the time necessary for pupation of prepupae collected on 17 May is presented in Fig. 12. The physiological age of prepupae on different collection dates strongly affected the rate of prepupal development. Prepupae collected 8 April, 1974 showed 50% pupation at 24°C after 26 days as compared to 16 days for prepupae collected 17 May, 1974 maintained at the same temperature. The conclusion that physiological ages affected development time was reinforced by comparing development of prepupae reared at 24°C and 16-hour light, 8-hour dark photoperiod (Fig. 13). The longer the time spent in the soil during the spring months, the shorter the developmental time. The mean number of days for pupation of prepupae collected 17 May, 1974 was 13.4 ± 3.2 days, as compared to 30.23 ± 8.17 for those collected 15 April, 1974 and 34.5 ± 12.9 for prepupae collected 14 March, 1974.

Soil temperatures of the litter soil interface at Big Star Lake were recorded for the spring of 1975 using a Weathervane (Model T-603-16) 31-day thermograph and are presented in Fig. 14. Temperatures did not exceed 12.8°C until 10 May, 1975. Pupation does not occur at temperatures below 12.8°C, but diapause intensity is reduced as prepupae remained in the soil.

The prepupal diapause was considered obligatory since all prepupae tested under "normal environmental stimuli" (i.e. those field-collected from litter and soil), exhibited some intensity of diapause. The diapause, however, was due to

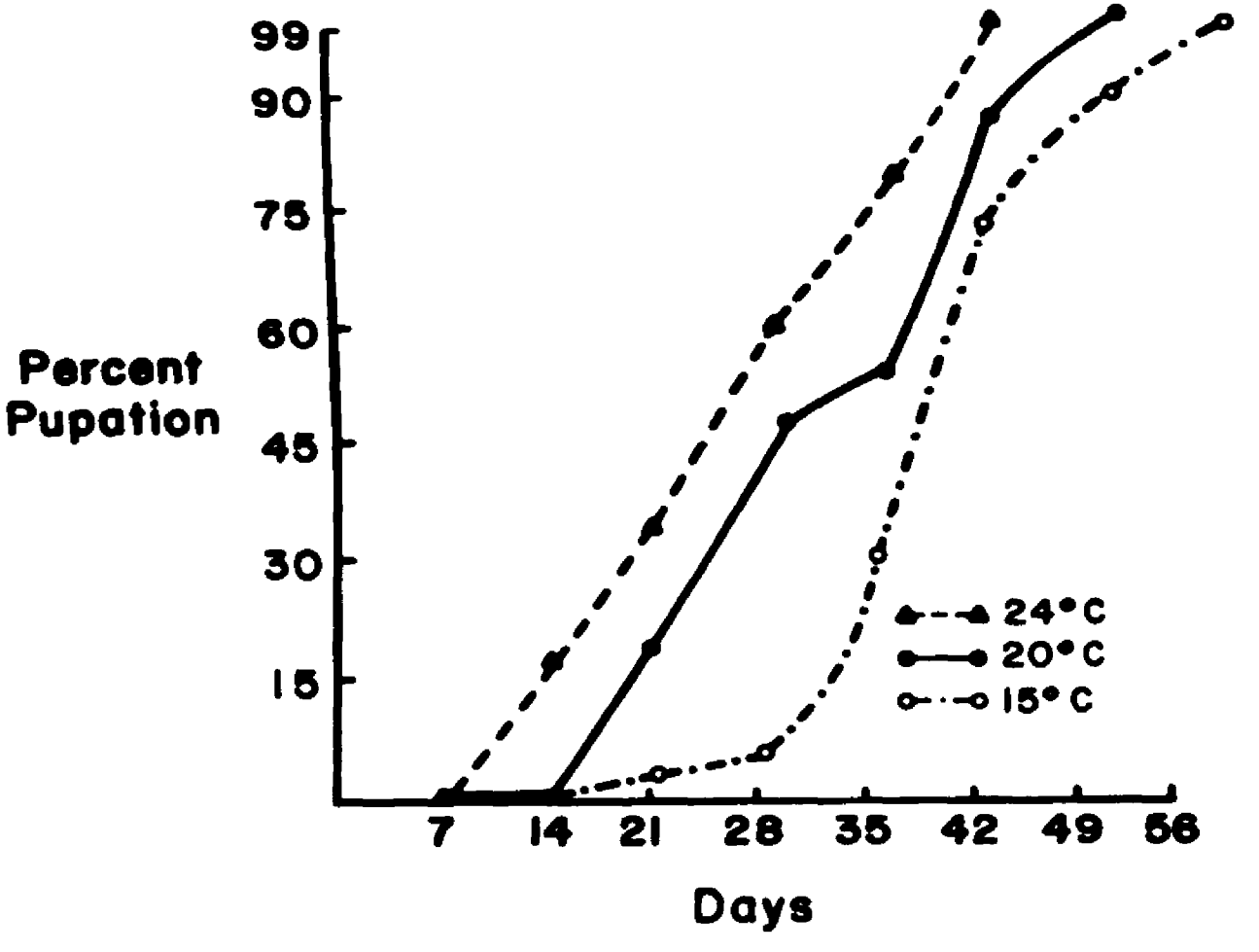

FIG. 11. The effect of temperature on development of prepupae of H. manteo collected April 8, 1974.

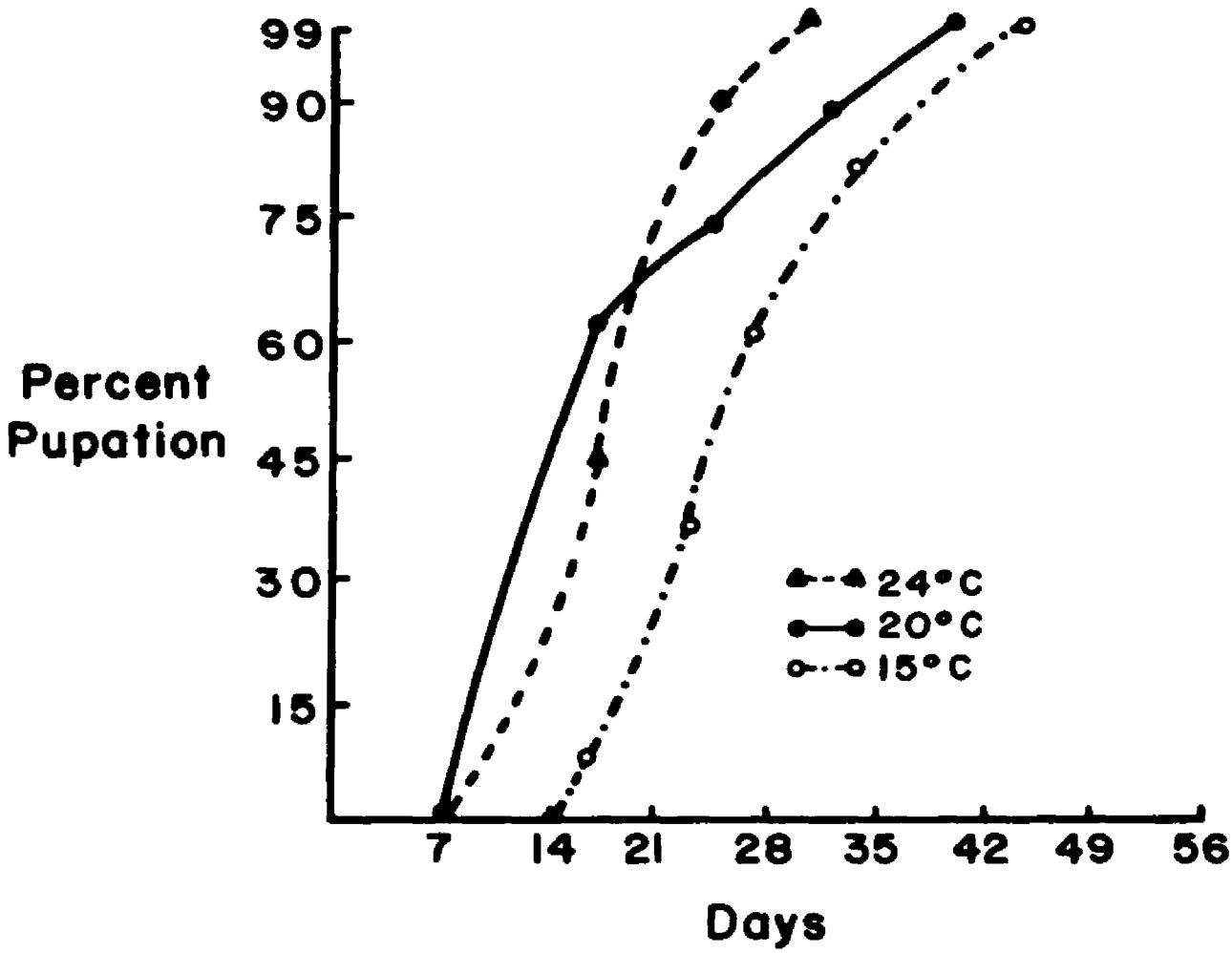

FIG. 12. The effect of temperature on development of prepupae of H. manteo collected May 17, 1974.

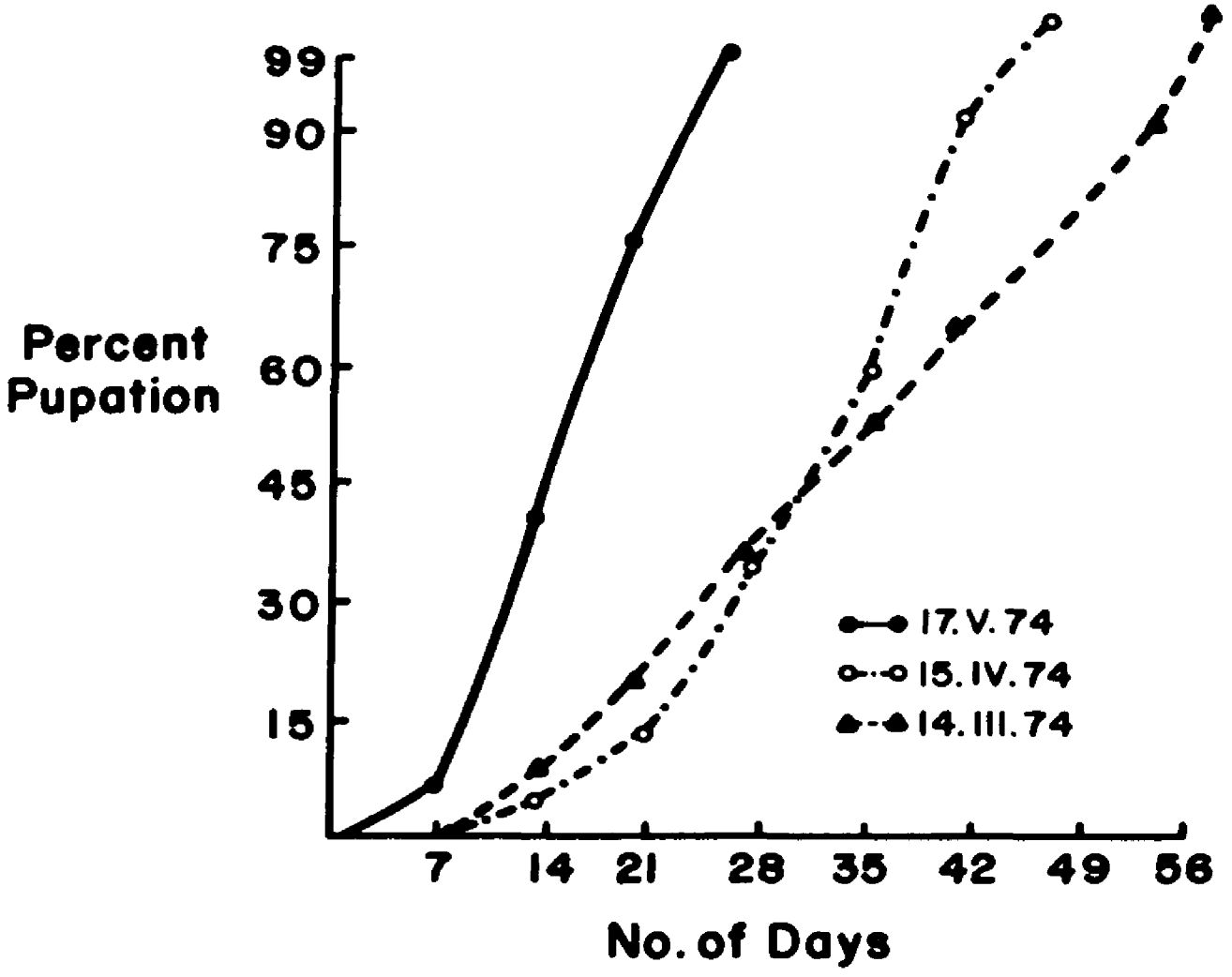

FIG. 13. Collection date as related to development of H. manteo prepupae maintained at 24°C.

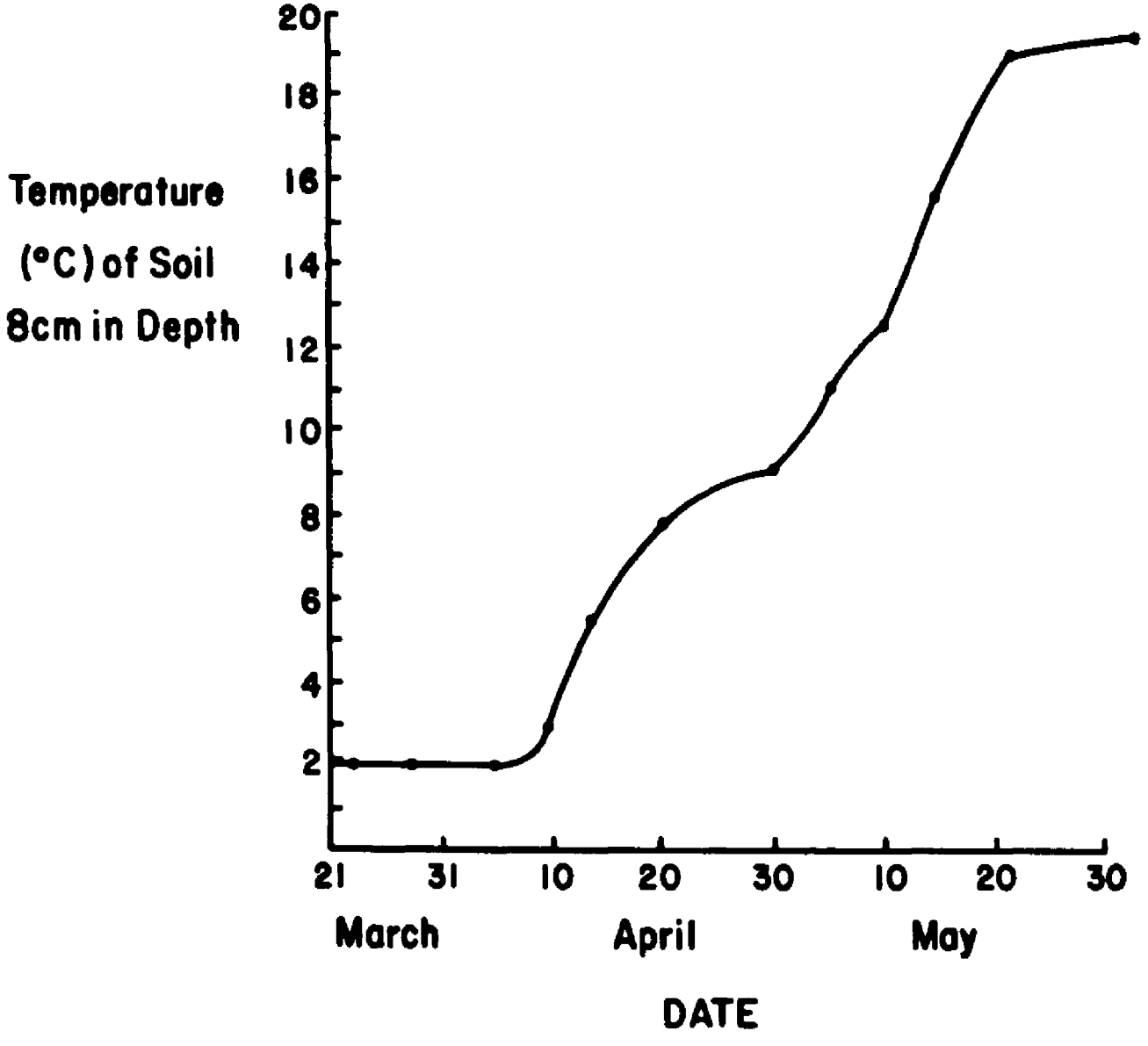

FIG. 14. Soil temperatures (°C) at 8 cm depth, Big Star Lake, Michigan, 1974.

some environmental factor since larvae reared in the laboratory under conditions of total darkness and temperatures of 20°C and 15°C pupated within 3 weeks of feeding cessation. Similarly, larvae reared at 24°C under a 16-hour light and 8-hour darkness photoperiod did not diapause. The environmental stimuli which initiated diapause was not examined, but I was of the opinion that diapause was under photoperiodic control. A short day cycle, i.e. 12 hours of light and 12 hours of darkness has been reported to initiate diapause in a large number of insects which overwinter in temperate climates (Dewilde, 1972). In the south 2 generations of H. manteo occur; larvae completing development in late June or early July do not exhibit diapause (Wilson, 1971). This reinforces the hypothesis that diapause is initiated by a "short-day" photoperiod.

During the spring of 1974, populations of prepupae were estimated by soil sampling. In all plots there appeared to be minimal overwintering mortality. Cone traps with a basal area of .25m^2 were placed on grid locations of all plots to monitor adult emergence. Adult emergence appeared considerably lower than expected, based on successful overwintering levels. Emergence was not, however, accurately determined because of extensive vandalism and wind damage to cone traps. After adult flight (as measured by black lights) prepupae existed within the soil directly beneath the cone traps. This presented evidence that a porportion of the prepupae did not pupate during 1974, but remained as viable pre-

pupae in the soil. Craighead (1950) and Wilson (1971) have both reported that some prepupae of H. manteo may remain dormant in the soil throughout an entire year.

Twenty soil samples were taken in each plot to determine the percentage of the prepupal population which remained in prolonged diapause. The timing of the samples was critical to ensure that: 1)prepupae in the soil would not emerge soon after the samples were taken, and 2)that prepupae discovered were from the previous year rather than newly dropped larvae.

Samples to estimate the percentage of the population in diapause were made during mid-August. At this time, adult emergence as measured by black lights had ceased and no viable pupae existed in the soil; only prepupae. In addition, when prepupal samples were taken, fifth instars were not present within the canopy. Throughout July, August and September larval development was monitored in the field using pyrethrum samples of entire oak trees (see larval development). It was assumed that if the mean larval instar did not exceed 4, then larvae which had completed fifth instar feeding had not existed within the canopy. Mean larval instar was determined as the average age of larvae taken from pyrethrum sampled trees. For example, if a spray resulted in a collection of 100 larvae of which 50 were third instars and 50 fourth instars, the mean larval instar was considered to be 3.5.

The results of soil samples taken in mid-August are presented in Table 11. Approximately 50% of the prepupal

Table 11. Prepupal densities and carry over population of H. manteo, Michigan, 1974-75.

Location	Spring Densities	August Densities	% 1974 Carry Over	Spring Densities	August Densities	% 1975 Carry Over
Big Star Lake	8.35	2.85	32.4%	5.35	2.55	47.9%
Newaygo	2.45	1.60	61.5%	1.75	1.05	60.0%
Branch Mature	3.10	1.55	49.6%	1.70	1.20	70.6%
Branch Pole	2.25	1.40	54.4%	2.05	1.35	65.0%
Dublin	1.40	.85	58.6%	1.45	.40	27.5%

population did not pupate during summer of 1974; and 55% did not pupate during the summer of 1975. This phenomenon is probably not unique to Michigan as evidenced by Anonymous (1958) who stated that in Virginia: "For reasons not wholly known, there was little or no emergence of adult insects despite the fact that prepupae were abundant in the soil during 1956-56." Problems in the determination of prepupal development are therefore additionally compounded because in any sample of prepupae the possibility exists that some have been in the soil less than a year, 2 years, 3 years or perhaps longer. No way to accurately differentiate the different aged prepupae was discovered.

During August of 1974 prepupae collected at Big Star Lake and Branch Pole plots were placed into plastic Mavjet^{R} injection capsules filled with litter and soil, and then buried to a depth of 5 cm. These prepupae were assumed to have originated from the 1973 defoliation by H. manteo since no fifth instars had yet been found in the canopy. In a similar manner, prepupae were placed into injection capsules during spring of 1975. On 28 August, 1975 the capsules, in all plots, were checked to determine the number of prepupae which had pupated. The results of this study are presented in Table 12. Some prepupae implanted in capsules during August of 1974 had still not pupated by August of 1975. These prepupae originated from the 1973 defoliation and remained viable for overwintering to 1976. The percentage of prepupae remaining in prolonged diapause was approximately 10% as determined by

those which diapaused in the capsules. This was misleading since the litter in most capsules had greater soil moisture and higher relative humidities than adjacent litter. Prepupae in dry capsules (equivalent to surrounding litter) were those which had not pupated.

In September 1975, 232 prepupae of known life histories (either reared in the laboratory or in field sleeve cages) were placed in open-ended soft-drink and beer cans. The cans were buried midway into the soil and duff and prepupae dropped onto the surface of the litter within the cans at the cessation of feeding. This allowed them to overwinter at their chosen depth and hopefully avoided the excess soil moisture experienced with injection capsules. In the spring, netting was placed over can tops and secured with rubber bands to hold emerging adults during the summer. The cans will be checked by students currectly on the project at the end of adult emergence in 1976 to determine the number of prepupae remaining in diapause. If necessary, cans will be monitored in future years to determine how long diapause may last under field conditions.

The diapause exhibited by prepupae in the fall after cessation of feeding is obligatory since the entire population manifests some diapause intensity. The diapause termination in the spring is facultative since not all prepupae behave alike. Prepupae collected in the early spring always pupated in the laboratory; but in the field approximately 50% of the population remained in the soil for a year or longer.

Table 12. Pupation of encapsulated prepupae of H. manteo examined 28 August, 1975.

Site	Date of Implantation No. Implanted	No Pupation	Pupated	Mortality Cause			% Mortality
				Fungus	Parasitoids	Ants	
Big Star Lake	Aug. 21/74 48	5(10.5%)	32	8	1	2	10.2%
Big Star Lake	May 20/75 88	3(3.4%)	76	6	3	-	10.2%
Branch Pole	June 6/75 32	10(31%)	17	5	-	-	15.7%
Branch Pole	Aug. 28/74 25	0%	23	2	-	-	8%
Newaygo	May 11/75 32	2(6.3%)	26	6	-	-	18.8%

The factors which caused the termination of diapause were not totally apparent. The prepupae have to be exposed to a threshold temperature greater than 12.5°C before pupation occurs, but some additional stimulus(i) is required to terminate diapause. This stimulus(i) must be applicable only during certain time periods. There exist "windows in time" during which some secondary stimulus(i) is required to initiate pupation. This apparently occurs in Michigan during May and June. If the stimulus is not received during this time period the prepupal diapause again intensifies and secondary stimuli will thereafter not initiate pupation until diapause intensity again declines. This would explain why pupation never occurs during July to October even though soil temperatures are above the threshold. The intensity of diapause was not as high for prepupae remaining in the litter and soil a second year. Prepupae collected in October of 1974 (a major portion of which were believed derived from the 1973 larval population) did pupate in the soil without being exposed to several months of cold temperature. These prepupae, however, required at least 40 days to pupate when held at 24°C.

Two critical questions concerning this theory of diapause intensity were not satisfactorily answered: what are the secondary stimuli which are necessary to terminate diapause and, what factors cause diapause intensity to again intensify? Several examples of Lepidoptera pupae and prepupae which remain in the soil for 2 years or longer have been cited by Powell (1974). He suggested that soil moisture was pro-

bably the critical factor which terminated diapause in those he studied. With prepupae of the pink bollworm, adult emergence and diapause cessation are strongly correlated with high levels of soil moisture following rains of .5 inches or more (Brazzell and Martin, 1959). Prepupae in Mavjet® injection capsules, which showed high levels of moisture, consistently pupated while those in capsules sealed such that soil moisture did not increase, did not pupate. This suggests that soil moisture or high degrees of relative humidity are secondary stimuli resulting in diapause termination.

The soils of the research area are extremely sandy (75%) with low water holding capacity. The leaf litter and associated humus acts to conserve most water reaching the soil surface. In years subsequent to major defoliation the leaf litter is greatly reduced and the water holding capacity is therefore reduced. This reduction in water holding capacity would increase the probability that prepupae do not achieve the critical secondary stimuli for diapause termination. Thus, in the years following major defoliations a large percentage of the prepupal population remains in prolonged diapause. This would prevent massive population outbreaks and thus consecutive defoliations. The insect would benefit because a complete collapse of the population due to starvation does not occur. In addition, the insect population is able to escape a large number of parasitoid species which have been increasing with the increase of the population of H. manteo (see larval parasitism as related to prolonger diapause).

Studies were conducted to determine if soil moisture affected diapause termination. Prepupae collected from Big Star Lake and Branch plots in April, 1976, were placed individually into 50 ml jars. Each jar contained 30 gm of oven-dried soil. The soil was dried at 100°C for 48 hours to ensure that all moisture was removed. Distilled water was added to create various percentage soil moistures by weight. The jars were then sealed with lids and maintained at 20°C and complete darkness for a period of 33 days. Twenty prepupae were tested under each moisture condition. The results of the soil moisture experiment are presented in Fig. 15. When the experiment was terminated, at the higher moisture levels of 22%, 20%, and 15%, over 90% of the prepupae had pupated. At the lower soil moisture levels of 12.5%, and 10% only 70% of the prepupae had pupated. Most of those prepupae which did not pupate at the lower moisture levels were dead because of desiccation. The experiment did not clearly demonstrate that high levels of soil moisture were a necessary stimulus for pupation.

In the laboratory prepupae in sealed jars consistently pupated. The only instance where prolonged diapause occurred was when prepupae were placed in a large 2m x 1m x 2m field cage. The bottom of the cage was lined to a depth of 10 cm with field-collected litter and soil. Prepupae collected, April 1976, were placed in the cage and allowed to form cells in the soil. The cage was maintained at 20°C with ca. 12-hour photo-period. Every 3 days the soil surface was watered.

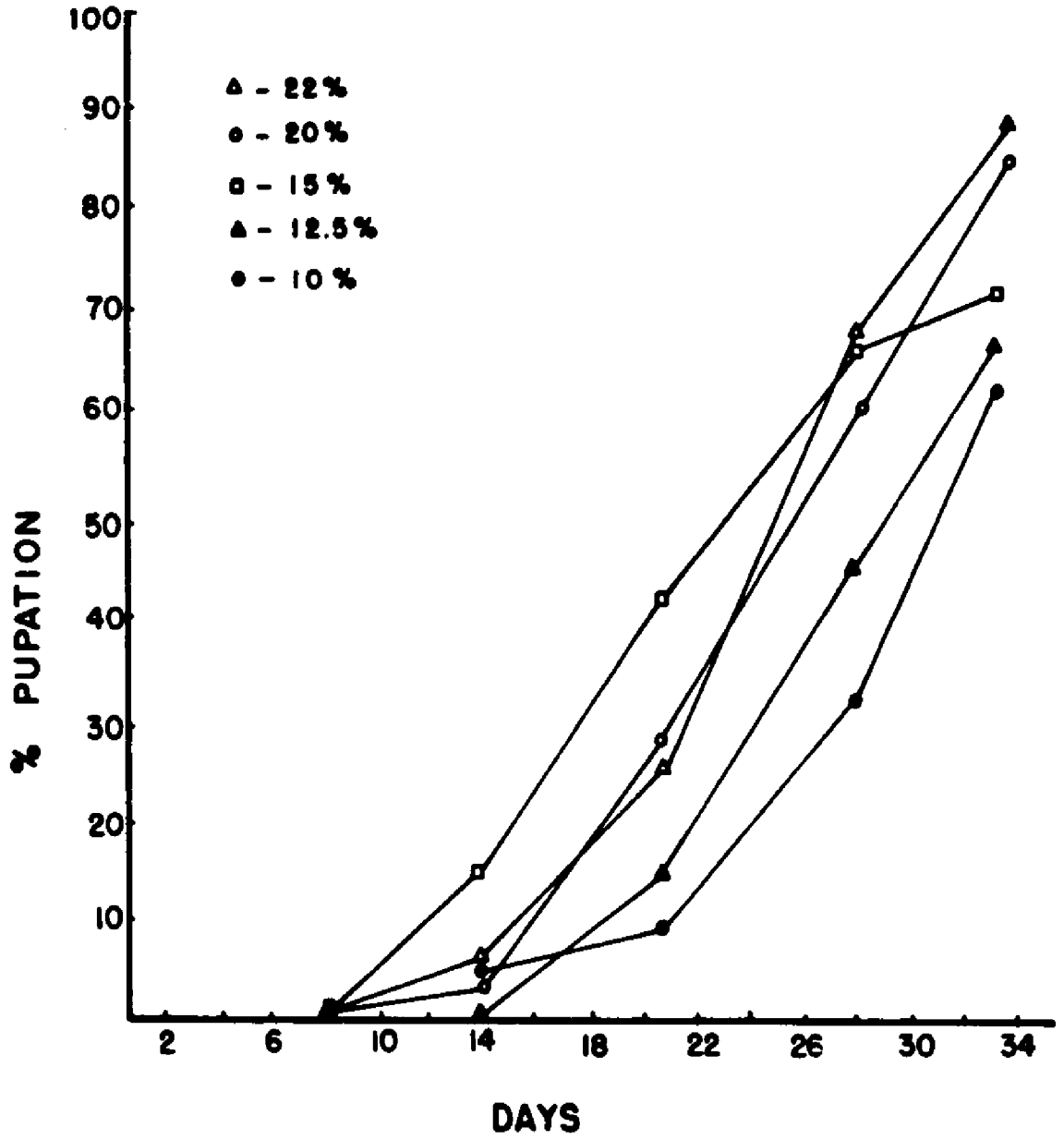

FIG. 15. Pupation of H. manteo under various soil moisture conditions.

Adult emergence began after 14 days and continued for another month. When adults emerged they were removed and tabulated. When adult emergence was completed the cage was left in place for an additional month, after which the soil and litter were removed and seived. Six of the 18 prepupae placed in the cage remained viable, but did not pupate. The environmental factors which allowed some prepupae to pupate and yet allowed 33% to remain in prolonged diapause were not determined.

Several possible factors are suggested. Prolonged diapause did not occur in those larvae which were held in sealed 50 ml jars. It did occur in a large cage perhaps because prepupae produce a compound which inhibits pupation of neighboring prepupae. This suggestion does not seem likely since precentage pupation does not appear to be dependent on prepupal densities (Table 11). Possibly, increased levels of CO_2 could initiate pupation. In the sealed jars the CO_2 is allowed to accumulate; whereas, in open cages the CO_2 can dissipate. The relative humidity of the air which prepupae intake may affect pupation. In sealed jars including those with low soil moisture, condensation could be seen on lids indicating high levels of humidity. In field cages relative humidity was assumed to be less.

The factor which caused prepupal diapause to intensify in July and August was not determined. A decreasing photoperiod in July and August may intensify diapause. Prepupae in the soil receive little light, but Dewilde (1962) reported that extremely low levels of light intensity could

cause diapause initiation. The probability of high moisture levels remaining for several days during July and August is remote. Diapause intensity could increase with shortening photoperiod and the probability of secondary stimuli also decreased as the summer season progressed. The theory of diapause for H. manteo is speculative. A great deal of experimentation is required to confirm or deny it. The insect, because of its size, abundance, ease of rearing and prolonged diapause presents an ideal organism for further investigations concerning diapause.

Pupal Sexing and Sex Ratios

Attempts were made to determine the sex of larvae and prepupae of H. manteo. No reliable method to sex larvae except by dissection for developing gonads or ovaries was discovered. Allen and Grimble (1970) were able to sex larvae of H. guttivitta in a similar manner. Separation of sexes prior to emergence as adults has practical applications. It may be invaluable for workers isolating sex pheromones and population ecologists determining sex ratios, particularly if adults of one sex are more difficult to monitor.

The pupae of H. manteo can be sexed by visible external characters found on the ventral side of the caudal segments. The genital opening is on the eighth abdominal segment in females and on the ninth in males. Packard (1895) and Ehrlich et al. (1969) have provided illustrations for sexual differentiation of pupae. A sex ratio of 1.12 to 1.00 males

to females was determined by examining and sexing 396 pupae. These were then reared until adult emergence. In all cases sex determination by pupal examination proved accurate.

Developmental Times of Pupae

Prepupae were examined daily to determine the date upon which pupation occurred. Once pupation had occurred, pupae were removed from 50 ml glass jars. They were placed on the soil and litter surface filling a 40 cm x 25 cm porcelain dissecting tray. Six pupae were spaced on each tray. A large block of wood was set beside each, and a 1000 ml beaker was inverted over the pupa and the wood. Every 3 days the litter surface was wetted with distilled water to maintain soil moisture. The inverted beaker was used to hold newly emerging adults and maintain higher levels of humidity. The relative humidity under inverted jars was approximately 70%. Newly emerged adults climbed onto the wooden blocks for drying and expansion of wings. Using this technique adults with excellent wing formation emerged over 95% of the time.

In several instances pupae were left in silken cells in the 50 ml jars to observe adult emergence. The adults emerged within the cells and immediately worked their way to the soil surface (4 cm) before wings began to expand. Once the surface was reached they climbed any vertical object and remained quiescent as the wings expanded and dried. The wing coloration is similar to that of tree bark (Fig. 18) and adults are difficult to observe on tree boles, upon which they climb in nature.

The effect of temperature on pupal development is presented in Table 13. The minimal temperature required for adult emergence was approximately 12.5°C since no emergence occurred at 10°C, but emergence did occur at 15°C. Pupae could be stored at temperatures of 4.4°C for periods up to 2 months without significant mortality. The duration of the pupal stage was not significantly affected by the sex of pupae.

The variability associated with pupal development was extremely small when compared to prepupal development, for apparently no type of diapause existed within the pupae. Each pupa was the same physiological age at the beginning of experiments; whereas the intensity of prepupal diapause varied among individuals. The date of adult emergence could be predicted with precision by knowing the date of pupation and the temperature regime to which the pupae were exposed. This knowledge proved useful in providing large numbers of male and female adults for pheromone studies. Pupae were stored at 4.4°C immediately after pupation, until the desired number of pupae was achieved. By regulating the temperature after removal from storage the desired date for adult emergence was achieved with reasonable accuracy.

In the laboratory the time necessary for adult emergence varied from 2 to 4 weeks depending upon temperature. Soil and litter temperatures were recorded during late May, June, and July of 1975 using a Weathervane® 3-point 31-day recording thermograph. The temperatures fluctuated between 16.6°C and 32°C throughout this time period which indicated

Table 13. Number of days to emergence for H. manteo prepupae maintained at various temperatures.

Temperature of Environmental Chamber	Mean No. Days until Emergence	
	Female	Male
24°C	15.1 ± 3.07	14.8 ± 4.8
20°C	20.3 ± 3.69	20.5 ± 3.96
15°C	29.6 ± 5.9	29.6 ± 5.28
10°C	No emergence	

that the pupal stage lasted 2 to 4 weeks in the field. In 2 instances newly formed pupae were monitored in the field and the pupal stage lasted 17 and 22 days. The peak adult emergence of H. manteo as measured by black light traps occurred about 25 July, 1973, '74 and '75. This indicated that most pupation in the field occurred about the first of July.

Flight Activity

Adult moths (Fig. 18) are cryptically colored similar to the bark of tree boles upon which they rest during the day. The adult stage has been described in detail by Packard (1895). Males can be readily distinguished from the females on the basis of antennal pectination, the males possessing the more pectinate antennae.

Adults are short-lived; in the laboratory they survive 4 to 7 days. They were kept in large screen cages and supplied with a water-molasses (50:50) solution upon which they were observed to feed. Females, however, readily deposited eggs without feeding on the molasses solution.

The adult moths are active during the night. The nocturnal activity of the adults was monitored by black lights during 1974 and 1975. Records of the number of moths obtained in black lights were kept from three locations: Big Star Lake, Newaygo, and Dublin. In both years adult emergence began about the first of July with peak emergence occurring about 25 July and adult activity ceasing by mid-August (Fig. 19, 20). Female catches were rare in black light traps, with

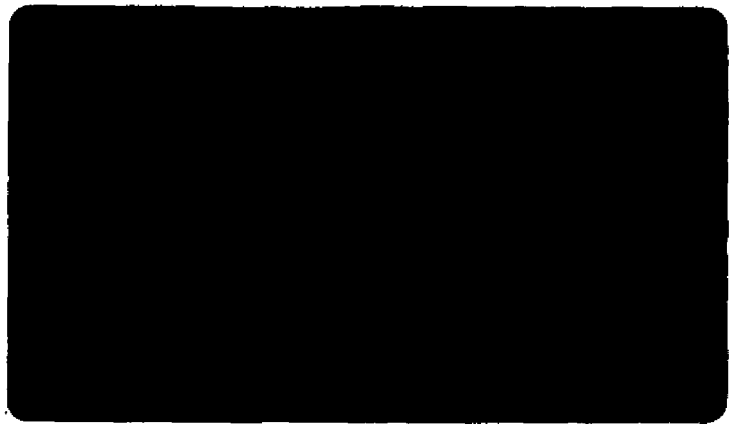

Fig. 16. Egg mass of H. manteo two days after oviposition showing red ring characteristic of viable eggs (Mag. 5x).

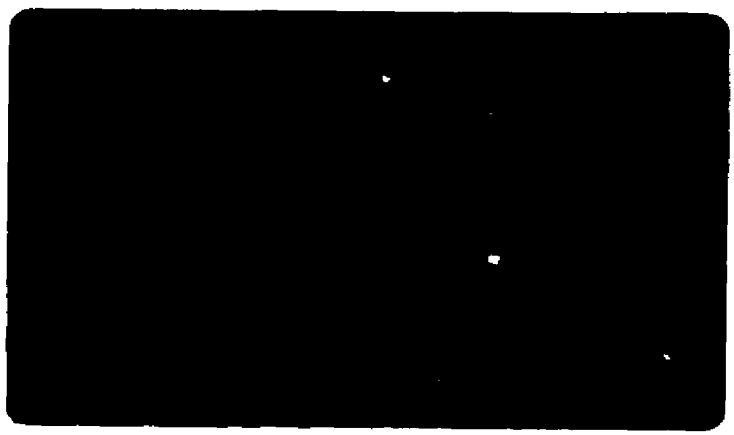

Fig. 17. Egg mass of H. manteo five days after oviposition showing first instar head capsules (Mag. 10x).

Fig. 18. Adult male of H. manteo showing typical color pattern of adults (actual size).

males outnumbering females by 33:1. Two evenings were spent monitoring nocturnal activity. At Big Star Lake during the evenings of 28, 29 July, 1975, black light catches were checked every 2 hours from 8 p.m. to 6 a.m. Adult moths were found in the 12 p.m., 2 a.m., and 4 a.m. checks, which indicated the activity of adults was nocturnal rather than crepuscular.

Fecundity Potential

Upon emergence adult females were found to be provigenic, the abdomen being completely filled with eggs. Laboratory females reared from prepupae collected in field samples were dissected to determine the potential number of eggs which could be laid by each female. The females were segregated by plot to determine if fecundity potential was dependent upon population density, i.e. prepupal density. Females were stored in 70% alcohol until the ovaries were dissected under a stereomicroscope.

The results of female dissections are presented in Table 14. The average number of eggs which could potentially be laid per female was 406 which is in agreement with Wilson (1971) who reported that each female may lay as many as 500 eggs. There was no significant difference in fecundity potential of females from various plots. The females from Big Star Lake which had the highest larval and prepupal densities did, however, produce the fewest number of eggs.

Individual gravid females were monitored in the labo-

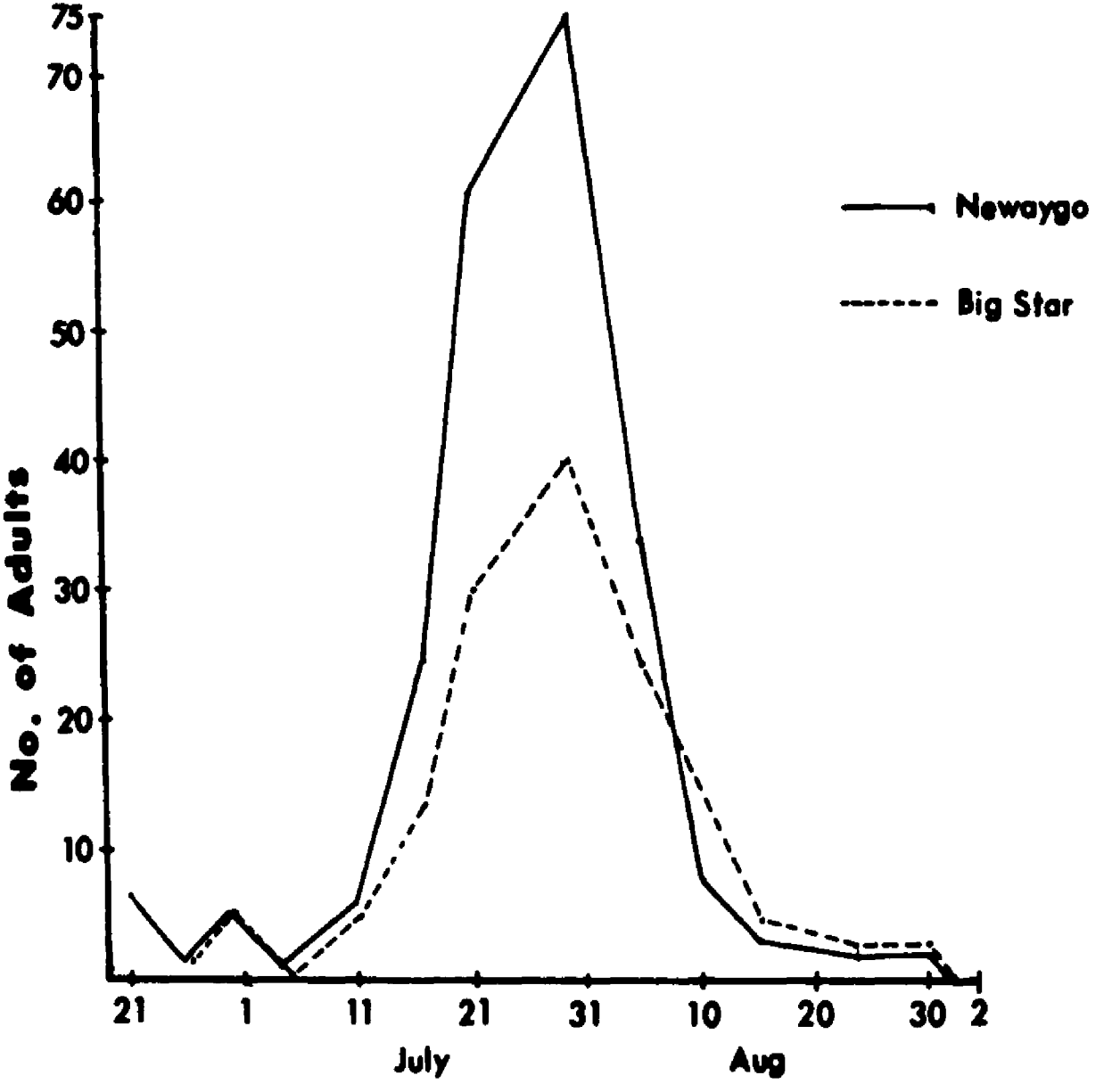

FIG. 19. Number of adults of H. manteo collected in black lights, Michigan, 1974.

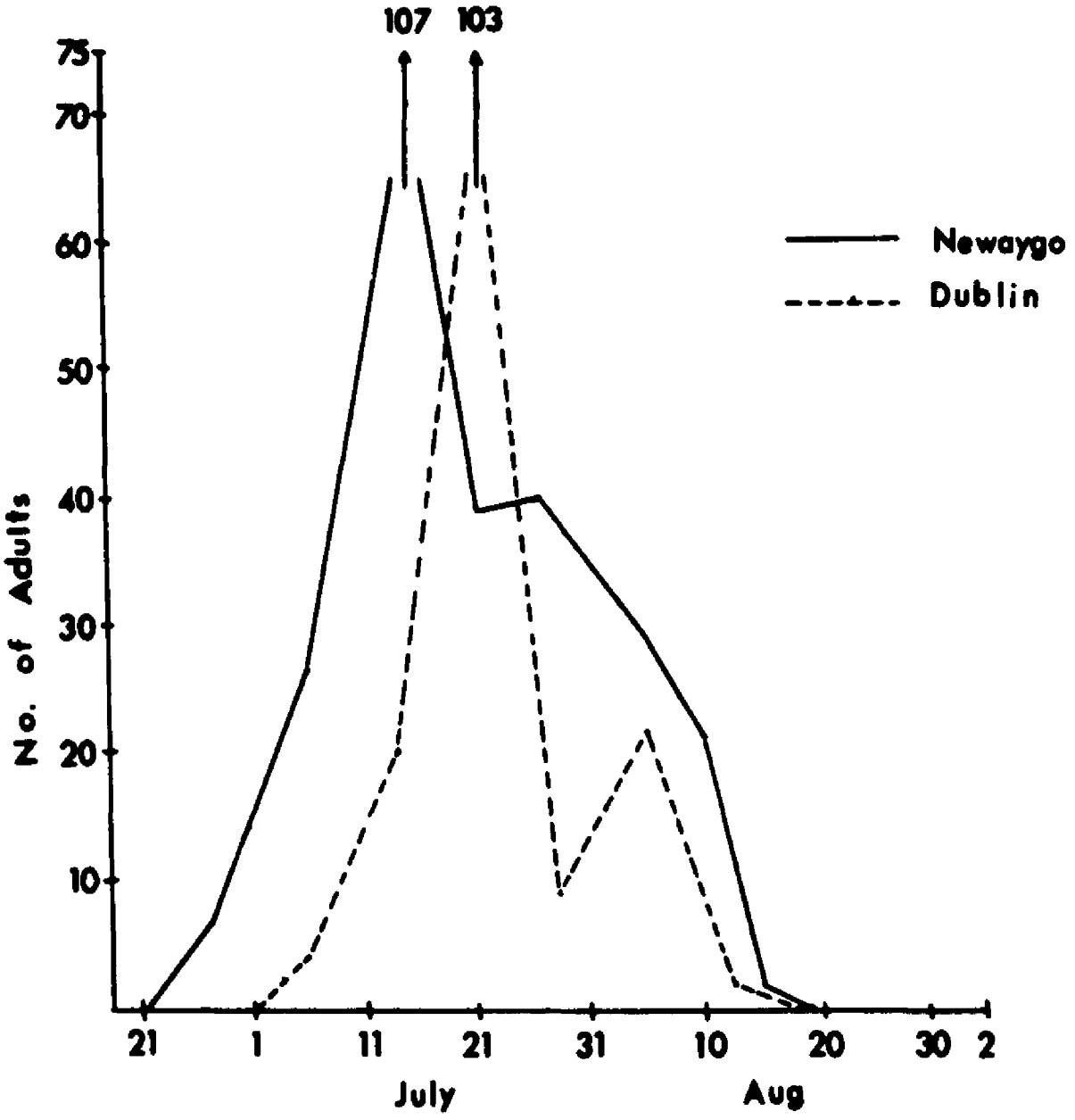

FIG. 20. Number of adults of H. manteo collected in black lights, Michigan, 1975.

Table 14. Number of eggs dissected from gravid females of H. manteo, Michigan, 1974-75.

Plot Location	$\bar{x}$ No. Eggs/Female	
Newaygo	377.6 ± 136.3	N=15
Big Star Lake	363.5 ± 141.9	N=23
Branch Pole	426.3 ± 168.3	N=12
Branch Mature	403.0 ± 81.5	N=8
Dublin	461.6 ± 126	N=11

ratory to determine the number of viable eggs produced. Only 5 females were observed to lay their complete egg complement, but the average number of viable eggs produced was 388.2 ± 86.71 which was closely correlated to that predicted by dissection. Fecundity mentioned above was determined under laboratory conditions, and most likely would be reduced under field conditions because of premature adult mortality.

Egg Laying Habits

Wilson (1971) based on descriptions provided by Packard (1895) reported that eggs of H. manteo were laid singly. Females in Michigan deposit eggs in large hemispherical masses (Fig. 17) on the underside of host foliage red or white oak. Despite careful observations no eggs were found on other tree species. To verify that egg masses were indeed those of H. manteo, larvae reared from eggs were sent to Dr. Franclemont, Cornell University, for identification, and adults reared from egg masses were identified by John Newman, Michigan State University. In both cases larvae and adults were identified as H. manteo. The earlier reports of eggs laid singly are believed to be due to misidentification of larvae and adults. They may have been those of H. guttivitta which does deposit eggs singly (Grimble and Newell, 1972b; Allen, 1973).

During the course of this study, 120 separate egg masses were examined in the field. The egg masses ranged in size from 10-350 eggs with a mean of 54.5 ± 44.7 eggs. This suggested that each female could lay about eight egg masses

during her adult life. A bimodal distribution of egg mass sizes existed with a large group of egg masses of a hundred eggs or more and another group of 20-30 eggs per mass. This suggests that females lay 1 or 2 large masses in addition to several small egg masses.

Development of Embryos

The eggs of Heterocampa manteo are light green (Fig. 16) when initially laid. Within 2 days a reddish band (Fig. 16) is evident upon the upper surface of the viable eggs. The eggs are hemispherical in shape (Fig. 21) with a smooth surface. The eggs have been described as begin "about 8 mm in diameter, hemispherical, shining under high power, irregularly hexagonally sculptured, the sculptures consisting of raised lines" (Packard, 1895). No evidence of hexagonal sculptures was observed on eggs in this study.

The time for embryo development lasts 4 to 9 days depending upon temperature. Embryos generally develop within 5 days at 24°C, 20°C, and 15°C; once the first instar head capsule develops (Fig. 17) eclosion occurs within 24 hours. The egg stage is short in duration. This confers a distinct evolutionary advantage since eggs are heavily parasitized by Trichogramma sp. and Telenomus sp. The short duration of the egg stage increases the probability that eggs will not be parasitized, since searching time of the parasitoids is reduced.

Egg Parasitism

Two species of insects, Trichogramma sp. (Trichogrammatidae) and Telenomus sp. (Scelionidae) were found to parasitize the eggs of H. manteo and the red-humped oakworm Symmerista canicosta Franclemont. Actual specific identification of these parasitoids proved impossible. Specimens were sent to personnel at both the U.S. National Museum and the Canadian National Collection. In both cases identification could not be made at specific levels.

Percentage parasitism was extremely high during 1974 as evidenced in Table 15. The majority of the egg masses were collected at ground level, while few egg masses from the upper canopy were examined due to the difficulty of sampling. The parasitism of egg masses from the upper canopy did not appear to be significantly different from those of the lower canopy. Allen (1972) reported that egg parasitism of H. guttivitta by Telenomus coelodasidis Ashm. and Trichogramma minutum Riley averaged 7 to 8% higher in the upper canopy of sugar maple and beech. Ticehurst and Allen (1972) have reviewed the biology of T. coelodasidis Ashm., the egg parasitoid of H. guttivitta. In New York the aggregate parasitism of H. guttivitta by T. minutum and T. coelodasidis was 40 to 78% (Allen, 1972). The extremely high levels of egg parasitism by Trichogramma sp. and Telenomus sp. in this study are therefore not unusual. Hanson et al. (1976) suggested that these parasitoids were responsible for the collapse of damaging populations of the red-humped oakworm and orange-humped

Table 15. Egg parasitism of H. manteo and S. canicosta by Trichogramma sp. and Telenomus sp., Michigan, 1974.

Site	# Masses	Total # Eggs	% Par.	No. Masses Telenomus	Parasitized Trichogramma
S. canicosta					
Newaygo	2	92	100%	2	2
Branch Pole	12	568	97.1%	9	8
Branch Mature	2	68	92.6%	2	2
Big Star	20	1033	91.6%	18	12
Dublin	49	2910	95.4%.	42	32
H. manteo					
Newaygo	2	100	90%	2	0
Branch Pole	11	557	75.2%	5	9
Branch Mature.	1	32	100%	1	1
Big Star	29	2851	84%	20	21
Dublin	6	376	82.6%	5	4

mapleworm, Symmerista leucitys Franclemont. Kearby (1975b) has suggested that egg parasitism was responsible for the collapse of H. manteo populations in Missouri. In Michigan, extremely high levels of egg parasitism contributed to the collapse of populations.

Where adequate numbers of eggs were examined, parasitism of S. canicosta eggs was consistently higher than parasitism of H. manteo eggs. This phenomenon was explained by the egg laying habits of the 2 species. S. canicosta lays its eggs on a single horizontal plane and when egg masses were examined they were generally totally parasitized as all eggs were accessible to adult parasitoids. In contrast, H. manteo deposits its eggs in large hemispherical masses (Fig. 16), eggs piled on top of each other. This proved significant in reducing egg parasitism since the inner core of eggs in large masses escapes parasitism as it is inaccessible to the adult parasitoids. The inner eggs hatch successfully, the outer eggs being parasitized. This phenomenon produces many egg masses which show a donut-shaped pattern as the larvae in the centers of the egg masses emerge. During the course of this study, most small egg masses were completely parasitized; whereas, in large egg masses ca. 20% of the eggs escaped parasitism (see egg parasitism) because the inner core of eggs was inaccessible to the adult parasitoids. There appeared to be a strong selection pressure against production of small egg masses or egg masses laid as a single layer.

In many instances, egg masses were found after parasitoids or larvae had emerged. It was therefore important to

differentiate eggs from which parasitoids or larvae had emerged. Eggs from which larvae successfully emerge are clear and generally broken in half. Parasitized eggs are always dark in color and the emergence holes left by the adult parasitoids determine which species has caused the parasitism. Trichogramma sp. leaves a small smooth-edged circular exit hole (Fig. 21A) and on several occasions 2 to 3 adult parasitoids were noted to have emerged from a single egg. Telenomus sp. produces an elliptical emergence hole, about twice the size of Trichogramma sp., about which strips of shredded chorion are found (Fig. 21B). In all cases Telenomus sp. proved to be a solitary parasitoid.

Parasitism levels of eggs appeared to be about equally distributed between Trichogramma sp. and Telenomus sp. Multiple parasitism was not observed. The adults are apparently able to distinguish eggs previously parasitized by their own species or other parasitoids. After completing oviposition the females of both species would drag their ovipositors over the egg surface apparently "marking" the eggs. Before females oviposit into the eggs they constantly tap the surface with their antennae apparently to detect previously parasitized eggs (Ticehurst and Allen, 1973). Adults of Telenomus fariai Lima can differentiate between parasitized and nonparasitized eggs (Rabinovich, 1970).

In 1974, the total egg parasitism for all 5 plots was 85% yet this figure dropped to 32% in 1975 (Table 16). This dramatic decline in parasitism was evident in all plots. The decline was apparently related to overwintering success of the

Fig. 21. Parasitized eggs of H. marteo illustrating adult exit holes.

A. Trichogramma sp.

B. Telenomus sp.

parasitoid populations. These parasitoids probably overwinter in alternate hosts although Kearby (1973) reported that Telenomus sp. parasitizing H. manteo overwintered as adults under the loose bark of trees. An unknown species of Telenomus does overwinter in the eggs of the white marked tussock moth Hemerocampa leucostigma (J.E. Smith) (Baker, 1972), a moth which was relatively common in the vicinity of the research plots. Members of the genus Trichogramma in general have a very broad host range which suggests the parasitoid of H. manteo may overwinter in some alternate host.

Massive population outbreaks of H. manteo are often associated with population increases of the red-humped oak-worm, S. canicosta, and the orange striped oak-worm, Anisota senatoria (J.E. Smith) (Beach, 1972). The life cycles of these are similar to that of H. manteo with the latter 2 species overwintering in the duff as pupae. There appears to be no prolonged diapause in these 2 species since pupae were never found in August soil samples. The egg parasitoids which attacked H. manteo eggs also caused high levels of parasitism in eggs of A. senatoria and S. canicosta. Egg parasitism appears to have been a major factor in the decline of populations of these defoliators. Removal of this parasitoid pressure may permit population increases. Generally, when 1 species of fall defoliator increases dramatically other species also become far more abundant (Beach, 1972). The parasitoid decline could be caused by a reduction in numbers of overwintering hosts (i.e. Hemerocampa sp. Malacosoma sp.). The populations of the fall defoliators may in fact be interrelated

Table 16. Egg parasitism of H. manteo by Trichogramma sp. and Telenomus sp., Michigan, 1975.

Site	Number of Eggs Examined	Percent Parasitism
Newaygo	2,253	36.1%
Branch Pole	1,348	31.8%
Branch Mature	None	---
Big Star	524	38.7%
Dublin	1,711	23.8%

to population levels of spring defoliators.

During the outbreak of 1973, 13 egg masses from Big Star Lake were collected by Thomas Ellis, Michigan State University. Twelve of the egg masses were parasitized by Telenomus sp. with a combined parasitism of 80%. Trichogramma sp. parasitized the other egg mass with 54% of the eggs being parasitized. In 1973, when major defoliation occurred, egg parasitoids, particularly Telenomus sp., were extremely abundant, causing heavy mortality. These levels of parasitism were not sufficient to prevent defoliation.

Larval Instars

Packard (1895) described 5 instars of H. manteo but these descriptions did not accurately match the instars found in Michigan. Determination of instars could not be based on larval coloration nor head capsule setal patterns because of extreme variability. Determination was therefore based on head capsule size (Surgeoner and Wallner, 1975) (see Appendix). A description of the larval instars is presented in Table 17 and figures of the various instar head capsules are presented in Fig. 22. Head capsule measurements showed 5 instars which was confirmed by rearing larvae from egg to adult in the laboratory. Other species of the genus Heterocampa have also been reported to develop through 5 instars (Klots, 1967; Allen and Grimble, 1970). First instars of H. manteo do not possess large prothoracic horns which is characteristic of other species of Heterocampa (Packard, 1895).

Table 17. Characteristics of instars of H. manteo larvae in Michigan.

Character	1st Instar	2nd Instar	3rd Instar	4th Instar	5th Instar
HEAD CAPSULE WIDTH (mm)	.40-.55 mm	.75-.95 mm	1.20-1.45 mm	1.65-2.25 mm	3.05-3.50 mm
BODY LENGTH	3-6 mm	5-9 mm	8-15 mm	15-27 mm	28-37 mm
DORSAL CHALAZAE	prothorax only	prothorax, abdominal segments 1 and 8			absent
HEAD CAPSULE COLORATION	Dark discolorations at the base of P_2, P_1, L, O and A_3 setae discoloration uniting AF setae forming inverted V.			Strong black band joining P_2, L, A_3 and A_1 setae.	
	Dark area forming between P_2 and L setae.				

Fig. 22. (a) First instar head capsule of H. manteo

(b) Second instar head capsule of H. manteo

(c) Third instar head capsule of H. manteo

(d) Top row (left) Normal fourth instar head capsule of H. manteo

(right) Normal fifth instar head capsule of H. manteo

Bottom row (left) Fourth instar head capsule of H. manteo parasitized by D. bethunei

(right) Fifth instar head capsule of H. manteo parasitized by D. bethunei

(e) Larva of D. bethunei in overwintering prepupa of H. manteo

(f) Pupa of D. bethunei with H. manteo prepupa in overwintering cell


e
f
3mm

Larval Feeding Habits

First instars of H. manteo are gregarious remaining close to the egg mass from which they hatch. They skeletonize the lower surface of the oak leaves on which the egg masses are found. Larvae feed in a straight line, all larvae touching each other and facing the same direction. This results in large areas of total skeletonization, rather than random patches skeletonized on the lower leaf surface. The presumed advantage of this behavior is to prevent fecal contamination of the host foliage; when larvae feed hanging upside down the feces always drops away from the leaf surface. In 1975, when parasitism of eggs was reduced the leaves on which these first instars fed were readily apparent in the canopy. These "flag" leaves were a dried brown color and contrasted markedly with the green canopy.

The coloration of the early instars is also variable, the overall body color being a light green with the dorsum generally having some red coloration. A common color type found in the canopy was for the larva to be overall green with a red stripe running along the dorsum of the thoracic and first abdominal segments. When disturbed the larvae readily drop from the leaves, although early instars generally remain attached by a silken thread. If the early instars were to drop to the forest floor a large proportion would likely never reach the foliage again. By contrast, fourth and fifth instars drop directly to the forest floor, rarely spinning a silken strand. They are mobile and reclimb tree boles to

seek out new leaves. The larvae of H. manteo are not considered to be highly dispersive. There is no evidence of deliberate migration, or wind dispersion as in the gypsy moth (Leonard, 1971). In 1974 and 1975 when larval populations were scarce, fifth instars could often be found in the vicinity of leaves where eggs had been laid. If the foliage supply is ample the larvae do not disperse, but remain feeding in the same area. It appeared from general field observation that the larval population in the lower canopies and on small shrub-sized oaks did increase as the season progressed. This was apparently due to larvae dropping from the higher leaves when disturbed by predators, wind, etc. and reclimbing to resume feeding.

Prior to molting larvae attach themselves to the underside of the leaf by producing a silken mat. These larvae are extremely vulnerable to predation as they can not drop from the leaves when threatened. In nature, the time spent attached to the leaves was about 24 hours for each molting period. From dissections of field-collected larvae I discovered that most individuals consume their exuvium after each ecdysis.

The second and later instars are solitary and feed along the leaf margins. The entire leaf except for a few major veins is consumed. As mentioned the later instars are often found feeding in the vicinity of old egg masses; but 2 late instar individuals were never found feeding on the same leaf. When collecting larvae in the field, if large numbers were placed in collection containers mortality of a

large percentage ensued within 2 to 3 hours. In these containers the odor of formic acid (see defensive secretions) was potent. Apparently the large instars were spraying formic acid when disturbed by other larvae and thereby contaminating the food supply and possibly killing larvae diredtly, since mortality after 2 hours was high. The solitary feeding habits of the later instars appeared necessary to prevent mortality of sibling larvae by spraying each other.

Laboratory Rearing

The rearing of insects in the laboratory is desirous since a great deal of basic biology may be determined from laboratory culture. In addition, laboratory rearing techniques are often necessary to create populations for control projects, i.e. sterile male, pheromone studies, parasitoid production. A technique was therefore developed to rear populations of H. manteo in the laboratory. The mortality associated with this rearing procedure was extremely low (5%). The disadvantages of the procedure are that it is time consuming and fresh oak foliage is required.

In the spring months prepupae were collected from the research plots by removing quarter meters of soil and litter. These prepupae were then placed individually into 50 ml jars and maintained at a constant 24°C until pupation occurred. Pupae were kept in jars until 5 days before expected emergence. Five male and 5 female pupae expected to emerge on the same date were placed in moist (18%) soil and litter lining the

bottom of a 45 cm x 30 cm x 30 cm screened cage. The pupae were buried in the litter to a depth of 3 cm. The cage was provided with a cotton swab moistened with a 50:50 molasses-water solution and several sprigs of white oak foliage were placed in the cage. Shortly after emergence adults mated and egg masses were laid on the oak foliage, but more commonly the sides of the cage. The eggs were left in the cages until they were determined to be viable by the development of a red ring (Fig. 16).

Eggs were then removed from the cage and placed in 50 mm x 20 mm petri plates lined with moist paper towelling. The eggs were held at 24°C until eclosion. The time necessary for eclosion was generally 3 days after the red ring was observed. When larvae hatched they were placed individually into 50 mm x 20 mm petri dishes for instars 1, 2 and 3. The larvae were provided with fresh oak foliage each day and reared at a variety of temperatures and photoperiods. The effect of temperature on the stadia is presented in Table 18. The duration of each instar was related to temperature, especially at temperatures below 20°C. The minimal temperature for development was approximated 12.5°C. First instar larvae kept at this temperature remained alive for 22 days, but never molted to the second instar. The fifth stadium was considerably longer than other stadia. When larvae developed to the fourth instar they were placed individually into one pint plastic containers where they were fed daily with red or white oak foliage. Up to 6 larvae could be reared in each container, but the mortality associated with rearing greater numbers

Table 18. Effect of temperature on stadia of H. manteo.

Temperature	Instar and Duration (days)					
	1st	2nd	3rd	4th	5th	Total
26.7°C[A]	3.56 ± .87	3.01 ± .80	3.30 ± .54	5.11 ± .89	10.65 ± 2.55	25.67 ± 2.55
23.9°C[B]	3.55 ± .91	3.38 ± .88	3.94 ± .89	5.30 ± .89	10.32 ± 2.22	26.94 ± 2.65
21.1°C[A]	5.09 ± .79	4.17 ± .81	6.21 ± .66	6.84 ±1.73	12.04 ± 1.73	34.55 ± 2.50
15.5°C[A]	7.43 ±3.56	7.77 ±1.33	7.90 ±1.33	10.40 ±1.82	18.47 ± 4.30	51.94 ± 5.11

A - complete darkness
B - 16-hour light, 8-hour dark photoperiod

together was significant.

When larvae were collected in the field from oak foliage and subsequently reared in the laboratory significant mortality occurred because of disease. Larvae infected were lethargic and excreted extremely watery feces. The causal organisms of the disease was not determined although it was not of fungal origin. When the disease developed in the laboratory cultures, infected larvae were removed and the rearing chambers and working area, used when feeding larvae, sterilized. A strong bleach was used for sterilization. The disease did not appear to cause significant mortality in nature, but was highly contagious in confined rearing chambers. The disease never originated in those colonies initiated from overwintering prepupae.

Parasitoids of Larvae

Seven insect species were found to parasitize larvae of H. manteo. These species included 3 tachinids, 3 ichneumonids and 1 braconid. The intensity of larval parasitism in 1974 was approximately 85%, with parasitism levels reaching 90% in the population epicenter at Big Star Lake. A brief description of the parasitoids and their relative significance is presented.

Tachinidae

Winthemia datanae (Townsend). Larvae of H. manteo were collected in all plots either by searching for the caterpillars on the foliage or by the use of pyrethrum samples

(see larval sampling). Parasitism rates in 1974 by W. datanae were less than 10% (Table 19) whereas in 1975 parasitism levels were less than 3% (Table 20). The adult parasitoid attacks the fourth and fifth instar larvae, depositing eggs directly onto the host. One or 2 eggs are generally laid, often on the dorsum of the thorax directly behind the host's head. This parasitoid is not host specific and has been reported to attack a wide variety of large Lepidoptera (Guimaraes, 1972). It is found throughout the U.S., Mexico and Canada. It overwinters as a larva in the prepupa of H. manteo. Pupation occurs the following spring during the period of normal pupation by H. manteo. Despite the fact that 2 eggs are often noted on the integumen of larvae only 1 parasitoid per host emerges.

Archytas atterimus (Rob.-Desv.). Parasitism by this species was less than 5% in 1974 (Table 19) and 1975 (Table 20) and it was therefore considered a minor parasitoid. The adults larviposit on the leaf foliage, the larvae being attached to the substrate. They wait for a suitable host to pass, at which time the parasitoid larvae attach themselves to the integument of the host and burrow into the larva. The reader is referred to Ravlin (1975) for a complete review of the taxonomy and biology of this genus. This species attacks a wide variety of Lepidoptera larvae including many species of Noctuidae and Notodontidae. It is found throughout the continental U.S.A. Those which parasitized H. manteo overwinter as larva within the prepupa. When host pupation occurs the A. atterimus larva kills the host and punctures

Table 19. Percent parasitism of H. manteo larvae, Michigan, 1974.

Sample Location	N	% Larvae Non-parasitized	% Parasitized D. bethunei	% Parasitized Phobocampe sp.	% Parasitized P. schizurae	% Parasitized by Tachinids
Newaygo	100	26%	34%	14%	20%	18%
Big Star	100	10%	35%	14%	41%	15%
Branch Mature	10	10%	20%	20%	20%	40%
Branch Pole	10	20%	20%	30%	10%	20%
Dublin	14	24%	18%	18%	6%	41%

Table 20. Percent parasitism of H. manteo larvae, Michigan, 1975.

Site	Number of H. manteo	Overall Para-sitism	Parasitoid		
			D. bethunei	L. schizurae	Other
Newaygo	253	13.8%	7.5%	5.1%	1.2%
Big Star	67	22.4%	18.6%	2.8%	--
Branch Mature	60	18.3%	9.2%	9.2%	--
Branch Pole	232	11.6%	4.3%	4.3%	3.0%
Dublin	594	16.6%	5.0%	10.0%	1.6%

the integument at the caudal end of the pupa. The puparium is then formed within the remains of the pupa and the adults emerge through the caudal openings made earlier by the larvae. Only 1 parasitoid per host is produced.

Lespesia schizurae (Townsend). This parasitoid caused less than 5% parasitism (Table 19) in 1974 and in 1975 parasitism rates were similarly about 5% (Table 20). The adults larviposit in chorion onto the host. A wide variety of lepidopterous larvae throughout North America have been reported parasitized by this species. The parasitoid overwinters as an early instar within the host and exits from the prepupa the following spring when normal pupation occurs. It was discovered, by rearing prepupae collected in August that this parasitoid remains in a prolonged diapause with the host. Evidently, if the prepupae of H. manteo remain in prolonged diapause so does the early instar larvae of L. schizurae.

Ichneumonidae

Barylypa sp. Parasitism rates by this ichneumonid were less than 1% in 1974 and 1975. Members of this genus oviposit into a variety of lepidopterous larvae. The parasitoid overwinters in H. manteo prepupae and emerges from the pupa. It is considered a minor parasitoid of H. manteo.

Phobocampe sp. Specimens of this parasitoid were sent to the Canadian National Collection and Dr. H. Townes, American Entomological Institute. No species identification was possible. Parasitism rates ranged from 14 to 30% in 1974, but were less than 1% in 1975. This insect therefore appears to be of major importance in reducing larval populations in

years after defoliation, but is probably poorly adapted for long term population control, particularly at low densities. The genus Phobocampe is reported to attack a wide variety of lepidopterous hosts including members of the genera Hemerocampa, Malacosoma, and Schizura (Meuesbeck et al., 1951). The insect is a solitary endoparasitoid which apparently oviposits into early instar larvae. The larva of the parasitoid emerges from the early fifth instar and pupates on the foliage by the larval remains. The pupa often drops to the forest floor soon after; if not, then does so when leaves drop in autumn. It therefore overwinters as a pupa on the forest floor. This insect destroys the host in the early fifth instar, and therefore helps to reduce levels of defoliation since over 85% of the foliage is consumed in the fifth stadium.

Diradops bethunei (Cresson). This insect was considered the major larval parasitoid with parasitism rates ranging from 18% to 35% in 1974 (Table 19) and from 5% to 19% in 1975 (Table 20). It is apparently host specific to H. manteo and found throughout the eastern and central United States. The parasitoid oviposits into first and second instar larvae and overwinters as an early instar (Fig. 22e) within the prepupae. Adult activity of D. bethunei as measured by number of adults collected in Malaise traps is presented in Fig. 23. Adult activity corresponded to the time when peak numbers of first and second instars of H. manteo were found. In the laboratory adult females readily attack first and second instars and viable colonies of D. bethunei can be reared in the laboratory by maintaining host larvae.

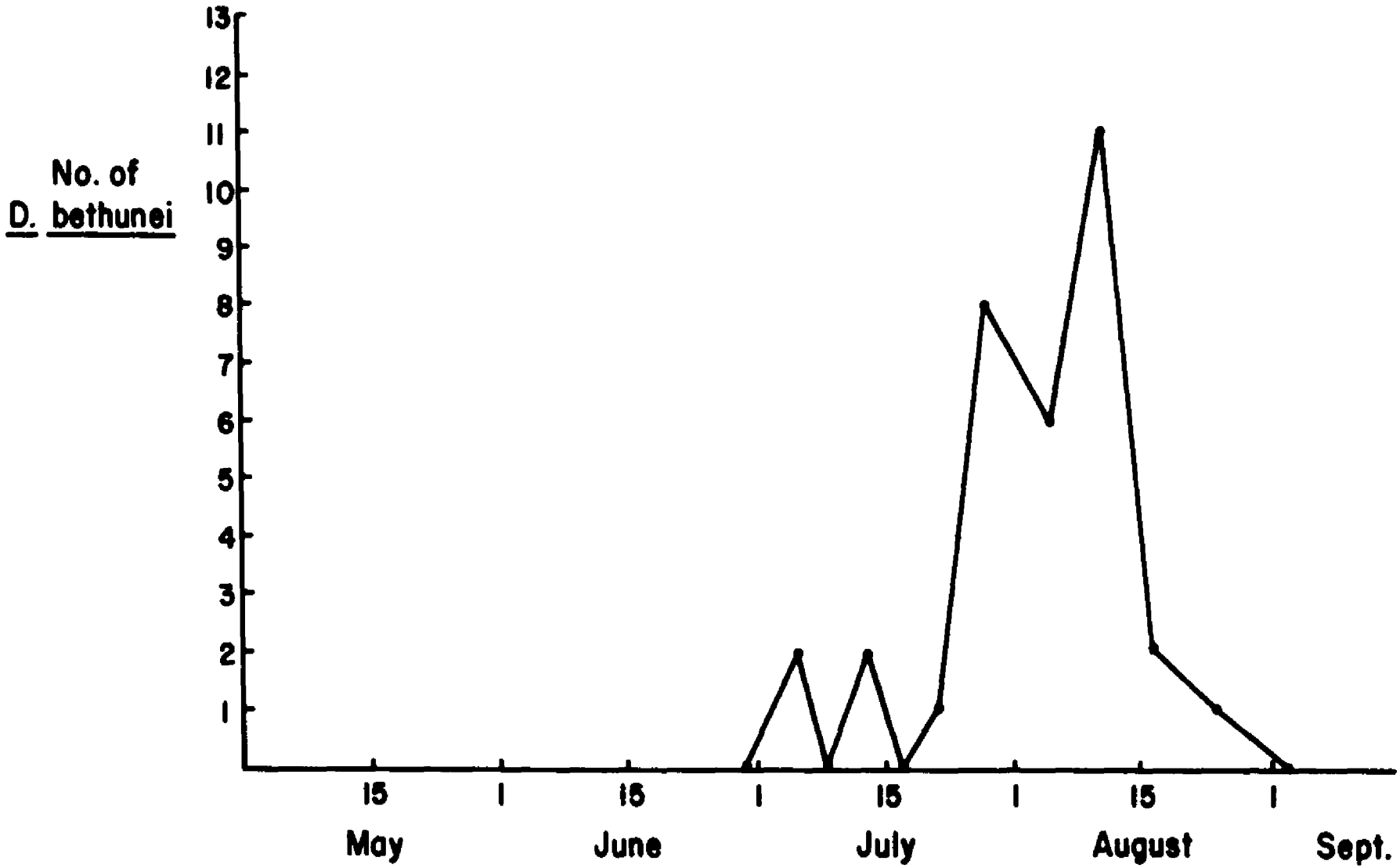

FIG. 23. Numbers of adult D. bethunei from Malaise traps, Big Star Lake, Michigan, 1974.

The prepupae parasitized by D. bethunei can be segregated on the basis of head capsule size (Fig. 23d) (Surgeoner and Wallner, 1975) and reduced body size (Fig. 3). In the autumn of 1973 and the spring of 1974 ca. 16% of the prepupae were parasitized by D. bethunei. In samples taken in mid-August of 1974 13% of the prepupae remained parasitized. This parasitoid had adapted to the prolonged diapause of the host. The parasitoid larva remains in the host and does not develop to maturity and pupate (Fig. 23f) unless it receives some stimulus from the host. This stimulus is probably a hormone secreted by the prepupae which initiates pupation. Larvae parasitized by D. bethunei consume 63% less foliage than non-parasitized larvae thus accounting for the reduced body and head capsule size. The parasitoid is of benefit, therefore, in not only reducing larval numbers but also in reducing the amount of foliage consumed.

Braconidae

Protomicroplitis schizurae (Meus.). This insect was classified as Microgaster schizurae by Muesebeck et al. (1951), but was identified as Protomicroplitis schizurae (Mues.) by W.R. Mason, Research Branch, Biosystematics Research Institute, Ottawa, Canada. The reported hosts include several other genera of Notodontidae. This is a endoparasitoid producing 1 to 14 larvae per host. The mean number of parasitoids per host was 6 at Big Star Lake and Newaygo in 1974. Parasitism rates in 1974 ranged from 6% to 41% and the insect was considered a major mortality agent of H. manteo. In 1975, however, the parasitism rates were less than 1%. The

parasitoid attacks the early instars and remains in the host until the prepupae drops to the soil. Once the prepupa forms the overwintering cell, it is killed, the parasitoid larvae exit, and spin silken cocoons in which they overwinter. The species is synchronized to a one-year life cycle since adults emerged, from all pupae examined, the following spring.

Multiple Parasitism

In 1974 approximately 14% of the larvae dissected were parasitized by more than 1 parasitoid species. No 1 species, however, was consistently found in multiple-parasitized larvae. The high level of multiple parasitism was apparently a consequence of extreme competition for H. manteo larvae since 85% were parasitized. Few hosts existed which had not previously been parasitized. In 1975, by contrast, when only 15% of the larvae were parasitized, less than 1% of the larvae were parasitized by more than 1 species.

Hyperparasitism

An ichneumonid hyperparasitoid Mesochorus vittator (Zetterstedt) was reared from pupae of Phobocampe sp. and Protomicroplitis schizurae. The specimens were identified by Dr. C. Loan, Research Branch, Biosystematics Research Institute, Ottawa, Canada. Accurate estimates of the level of hyperparasitism proved impossible because M. vittator larvae develop within parasitoid larvae. Thus, dissection of H. manteo larvae does not reveal hyperparasitoid larvae since they remain within the larvae of the primary parasitoid. The 2 species which M. vittator attacked were extremely rare in 1975. M. vittator may have contributed to the decline of

these parasitoid populations. Adults of Mesochorus sp. were never reared from other parasitoid species although species in the genus commonly parasitize a wide variety of parasitoids (Muesebeck et al., 1951).

Parasitism as Related to Prolonged Diapause

The percentage parasitism of H. manteo larvae in 1974 (84%) and 1975 (16%) is presented in Fig. 24. It was evident that not only was there a dramatic decline in parasitism rates, but that only 2 parasitoid species caused any significant levels of parasitism in 1975. These 2 parasitoids were Diradops bethunei (Cress) and Lespesia schizurae (Townsend), both of which could successfully remain in prolonged diapause within their hosts. For example, when prepupae in prolonged diapause were collected in mid-August only these 2 parasitoids were reared from the prepupae. Other parasitoids are apparently synchronized to a one-year life cycle.

The majority of the prepupae which overwintered in 1974-75 were derived from the 1973 defoliation, as larval populations were extremely low in 1974. Only D. bethunei and P. schizurae were able to successfully maintain themselves in the diapausing population while the other parasitoids were forced to overwinter on the small numbers of larvae developing in 1974. In the spring of 1975 the other parasitoids were few in number while the 2 parasitoids synchronized to the prepupae emerging after 2 years did remain in numbers sufficient to cause measurable parasitism.

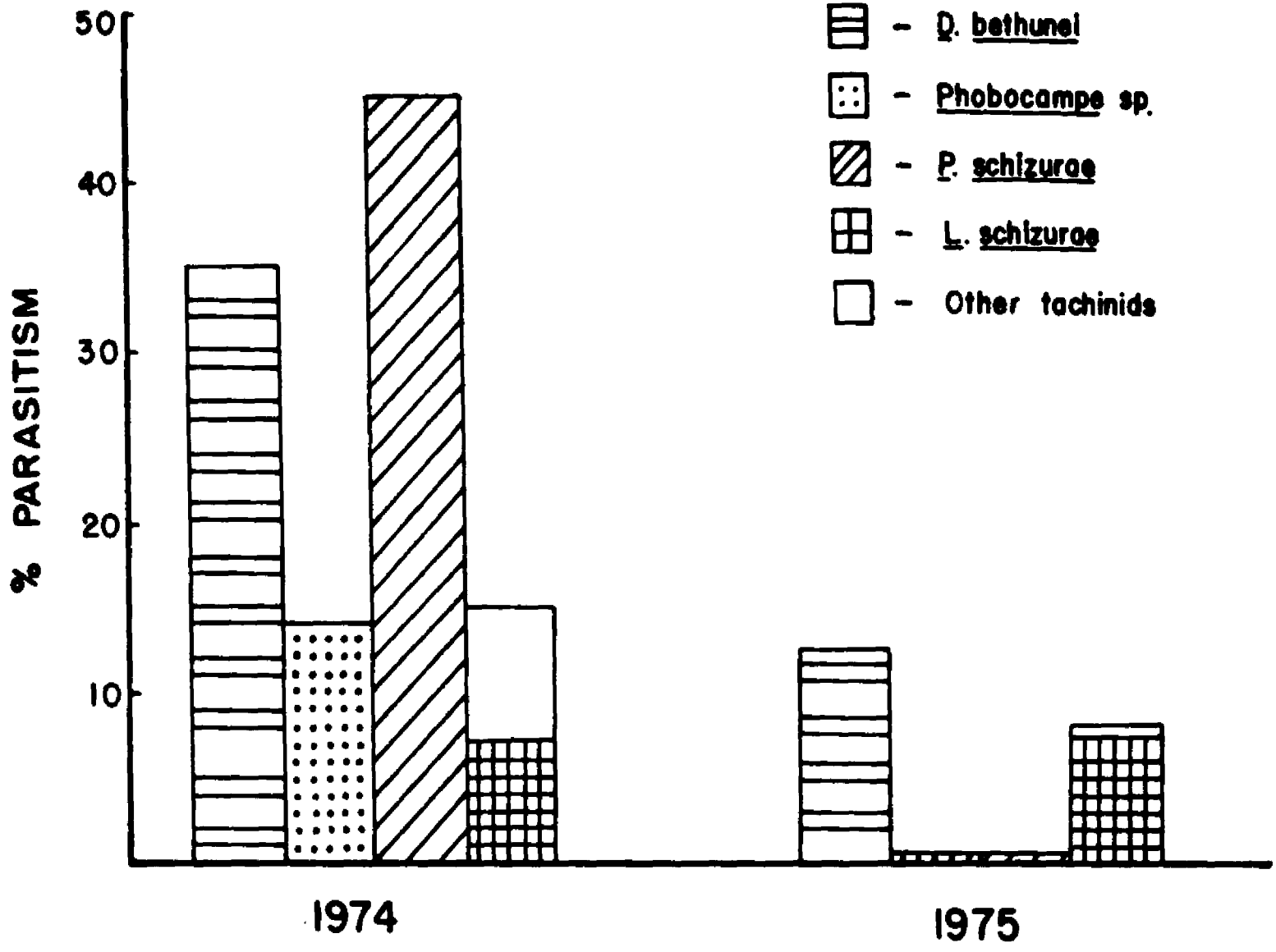

FIG. 24. Percent parasitism of H. manteo larvae, Michigan, 1974-75.

The parasitoids synchronized to a one-year life cycle contributed to the collapse of the defoliating population. These parasitoids, because of their poor synchronization to the two-year life cycle, do not cause high levels of parasitism in low density populations. The two parasitoids, D. bethunei and L. schizurae which may remain 2 years or longer within their host should be considered most suited for long term population regulation at low densities.

Predation

No insects were observed to feed on the eggs of H. manteo, but a number of species were observed to feed on the larvae. The early instars appeared most susceptible to predation as later instars were either too large or able to better defend themselves with formic acid secretions. Species of the following families were observed to feed on early instars of H. manteo:

1) Adults and nymphs of Reduviidae
2) Adults of the family Cleridae
3) Adults and nymphs of Pentatomidae
4) Larvae of Chrysopidae
5) Adults and larvae of Carabidae (in particular, Calosoma sp. and Pinacodera sp.).

Only the large predaceous ground beetles Calosoma scrutator Fab. and C. frigidum Kirby were observed to feed on late instars. Hooker (1908) reported that in Texas adults of Calosoma were found to feed on larvae of H. manteo. The

impact of insect predators on populations of H. manteo was not determined. I believe that perhaps 15% to 25% of the early instars are destroyed by the predators and less than 5% of the later instars. These percentages were based on general field observations over a three-year period and not on experimental evidence.

There was little evidence of vertebrate predation of H. manteo larvae. This may have been due to the large quantities of formic acid found in the defense gland of the larvae and prepupae. In the autumn and spring of 1974 and 1975 acres of the forest floor showed signs of digging and scratching by the wild turkey Meleagris gallopavo Vieillot. Consequently, in March of 1975, 12 turkeys shot during the local hunting season in Lake County were dissected. These birds were brought to the Department of Natural Resources check in center at Baldwin, Michigan. With the permission of the hunters, the crops and gizzards were removed and their contents examined under a stereomicroscope. In 1 individual the remains of a single prepupae was discovered. The turkeys did feed on the prepupae, but the numbers consumed was believed minimal.

Sampling of Larval Populations

A sample technique was required to determine relative larval densities and to monitor instar development. The canopy of entire trees was sprayed to determine the number of larvae per tree and the age distribution of larvae. By spraying complete trees one avoided the difficulty of collecting

caterpillars in the upper canopy. The undergrowth beneath trees which were to be sampled was removed with the aid of an axe. A 225 ft^2 tarp was then placed beneath the canopy. The tarp was constructed in two equal sections which snapped together along a mid-seam. Four stakes elevated the corners of the tarp and created a concave surface. Thus all insects which dropped to the tarp remained on the surface and were collected and stored in pint jars containing 70% ethyl alcohol.

The trees were sprayed from atop a 12.15 m ladder mounted on a truck. The trees were sprayed using 4.5 liters of spray solution containing .141 of 0.5% (AI) pyrethrum applied using a KWH S-66 m knapsack sprayer. The canopy of the tree was completely covered with spray solution using this technique. The tarp was left in place beneath the trees for ½ hour after spraying at which time the insect fauna were collected. Wallner (1971) has described a similar spray technique for evaluating insecticide efficacy.

The larvae collected using this technique were classified as to instar and dissected to determine the parasitism levels of the population. An extremely high variability between trees existed and the technique could not be used to accurately define densities per plot. The method did show the relative difference of densities between years. The population at Big Star Lake in August 1973 averaged 1083 ± 516.4 larvae per tree; by contrast the populations in August of 1974 and '75 were 16.3 ± 11.7 and 19.8 ± 13.5 larvae per tree respectively. This sampling technique did show the massive

collapse of the population between 1973 and 1974. By determining the mean larval instar in each sample it was also possible to monitor larval development through the growing season (Fig. 25).

Foliage Consumption by H. manteo Larvae

Overwintering densities of prepupae do not provide an accurate method for predicting defoliation because a significant portion of the prepupae may remain longer than 1 year in the litter. It is also difficult to predict defoliation by egg mass densities since egg parasitism by the parasitic hymenoptera Trichogramma sp. and Telenomus sp. has proven to be as high as 90% in Michigan. The density of early instars on foliage is the most reliable parameter for predicting defoliations. Estimation of defoliation is essential when formulating control strategies and must be based upon foliage consumption by individual larvae. A study was therefore conducted to determine the amount of foliage consumed by various instars and the effects of host plant, temperature and parasitism upon foliage consumption were also investigated.

Instars were reared according to previously outlined laboratory rearing procedures. The foliage used for feeding trials was taken from several red and white oaks situated on the Michigan State campus. The environmental conditions used in this study are presented in Table 21. The foliage fed to individual larvae was changed daily and before adding new foliage the leaf outline was traced on 25 mm grid paper.

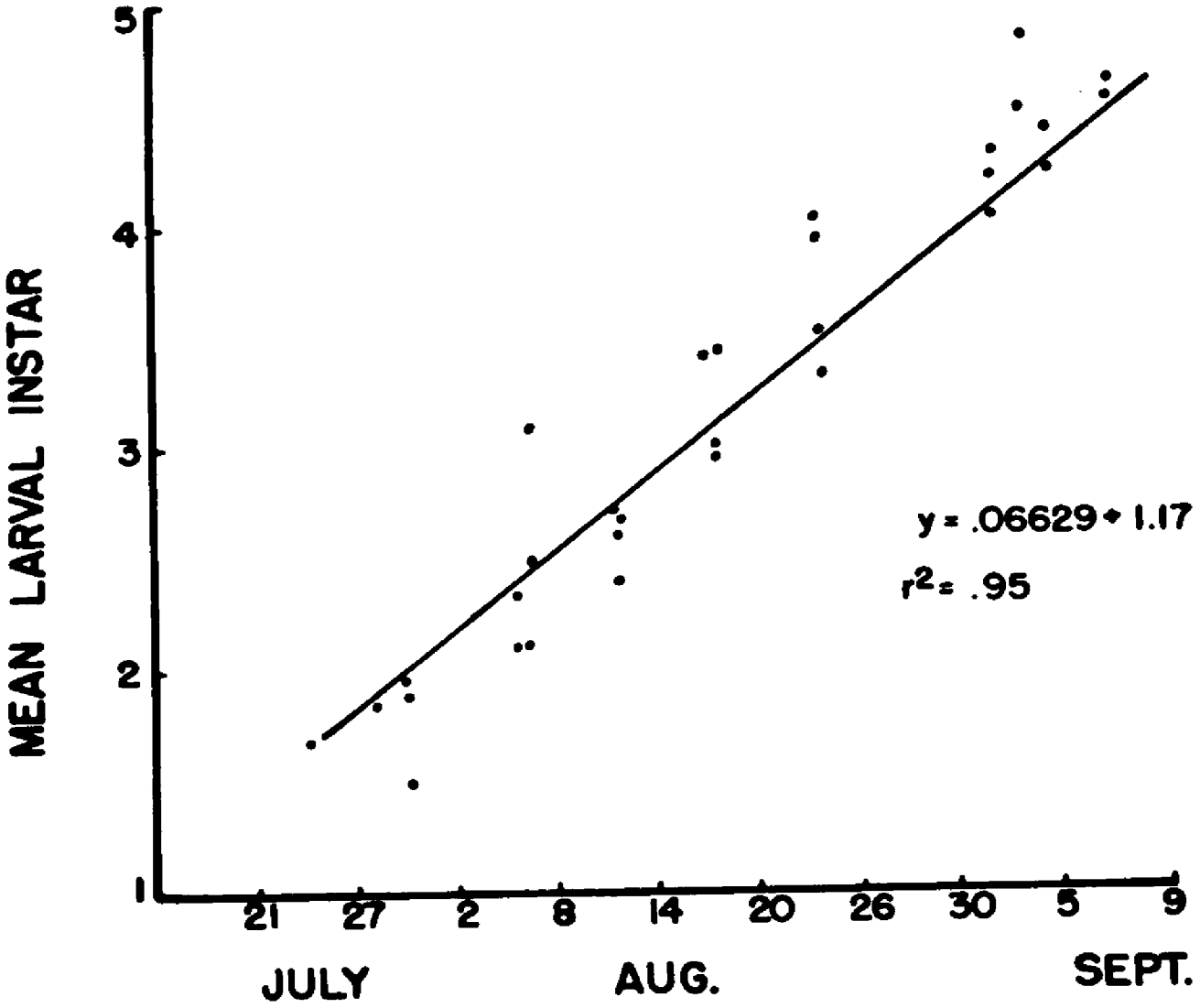

FIG. 25. Mean larval instar of H. manteo in pyrethrum spray samples, Big Star Lake, Michigan, 1975.

Table 21. Rearing regimes for H. manteo used in study.

	No. of Larvae Reared				
	Host				
Temperature	Q. alba	Q. borealis	Parasitized	R.H.	Photoperiod
26.7°C	16	12	5	60%	complete darkness
23.9°C	25	25	14	60%	16-hour light
21.2°C	11	20	3	60%	complete darkness
15.5°C	11	10	0	60%	complete darkness

When foliage was removed the outline of the remaining leaf area was subtracted from that of the original and daily consumption for each instar was tabulated. Small fragments of foliage eaten from leaves, but not consumed were considered part of total consumption. When predicting defoliation these fragments represent leaf area which is removed from the tree thus increasing the level of defoliation. Approximately 10% of the foliage consisted of this type which is in close agreement for that determined for the gypsy moth P. dispar (Brahman, 1975).

Larvae used to investigate the effect of parasitism were placed as first instars into 45 cm x 30 cm cages along with 2 male and 2 female Diradops bethunei (Cress). After 3 days larvae were removed and reared in the same manner as non-parasitized larvae. The foliage consumption of first instars parasitized by D. bethunei was assumed to be that of non-parasitized larvae, since eggs of D. bethunei do not hatch until larvae reach second instar. Parasitism was confirmed by reduced head capsule size of fifth instars (Surgeoner and Wallner, 1975).

The effect of host plant on foliage consumption is presented in Table 22. Analysis of variance showed that there appeared to be no significant difference in consumption of larvae reared at 21°C, 24°C and 27°C; because of this, larvae reared at these temperatures were pooled for this comparison. There was no significant difference in total foliage consumed whether northern red oak or white oak; early instars consumed more white than red oak foliage which is not surprising since

Table 22. Consumption of foliage from two Quercus sp. by instars of H. manteo.

	Total Consumption (cm^2)/Instar					
	1st	2nd	3rd	4th	5th	Total
Q. borealis	.52 ± .17	1.55 ± 40	6.86 ± 1.79	36.13 ± 9.55	288.3 ± 65.03	333.4 ± 67.84
Q. alba	.70 ± .29	1.88 ± .53	9.31 ± 3.08	45.09 ± 12.04	277.5 ± 40.87	334.5 ± 42.51

white oak is the preferred host (Wilson, 1971).

The effect of temperature on foliage consumption is presented in Table 23. Because foliage type did not significantly affect consumption, larvae reared on white oak or red oak were pooled for this analysis. No significant difference occurred in foliage consumption at temperatures of 21°C, 24°C or 27°C; however, larvae reared at 15°C consumed significantly ($P. < .05$) less (42.6%) foliage.

Raham (1970) showed that larvae of Pieris rapae consumed significantly more food when reared at 22.5° as compared to 24.3°C. This was apparently due to the increased duration of feeding. The fifth stadium of H. manteo was significantly longer ($P < .05$) at 15°C than other temperatures (Table 18), but daily consumption was 73% hower than that of higher temperatures. Larvae reared at 15°C were capable of normal development although adults were reduced in size. Mukerji and Guppy (1970) have shown that when rate of food intake is low in Pseudaletia unipuncta (Haw.) there was a reduction in fecundity. Prelimimary studies indicated that fecundity of H. manteo reared at 15°C was lower than other temperatures.

The effect of parasitism by D. bethunei on larval consumption is presented in Table 24. Parasitized larvae consumed 61.3% less foliage than non-parasitized ($P < .01$). This reduced consumption is correlated with lower weight and smaller head capsule size (Surgeoner and Wallner, 1975).

Predicting Defoliation

The ultimate objective of the feeding trials was to

devise a method to predict defoliation. Two possible methods are presented. The first involves the amount of foliage consumed by first instars. Adult females deposit eggs in large clusters of 30-300 placed on the underside of oak leaves. The first instars feed gregariously, skeletonizing the lower leaf surface. Leaves, from which non-parasitized egg masses have developed, are readily apparent since the lower leaf surface is completely skeletonized. These "flag" leaves may be seen 20 m into the canopy and verification of H. manteo feeding is made by the presence of hatched eggs which adhere to the leaf. From the data provided in Table 22 first instar feeding on white oak represented .0021 of the total consumption; whereas on red oak first instar feeding represented .0015 of the total consumption. It is possible to predict defoliation by the level of first instar skeletonization. If 0.1% of the white oak foliage is skeletonized the expected defoliation would be $\frac{.1\%}{.0021}$ or 47.6% whereas if .1% of the red oak foliage is skeletonized expected defoliation would be $\frac{.1\%}{.0015}$ or 66%. This method for predicting defoliation assumes that all first instars survive to complete development and that all first instar skeletonization is detectable.

Over 85% of the foliage consumed by H. manteo is by fifth instars. It is possible to predict the ultimate levels of defoliation based on relative density of larvae/leaves. In the research areas the total foliage consumed (i.e. 334 cm^2) was converted to number of leaves consumed. Based on 30 leaf

Table 23. Effect of temperature on consumption of oak foliage by instars of H. manteo.

	Temperature and foliage consumed (cm^2)/Instar			
Instar	27°C	24°C	21°C	15°C
1	.59 ± .28	.52 ± .16	.63 ± .23	.66 ± .22
2	1.89 ± .67	1.66 ± .46	1.73 ± .47	1.55 ± .61
3	9.29 ± 3.49	7.58 ± 2.19	7.45 ± 2.19	6.60 ± 1.5
4	44.78 ± 11.66	37.41 ± 10.07	40.25 ± 12.75	30.93 ± 11.58
5	286.59 ± 44.70	270.70 ± 47.09	297.06 ± 47.22	153.03 ± 47.30*
Total	343.1 ± 46.57	317.8 ± 48.05	347.1 ± 52.89	192.53 ± 53.3*

*Significant at the .05 level.

Table 24. Consumption of oak foliage by non-parasitized larvae of H. manteo and those parasitized by D. bethunei.

	foliage consumed (cm^2)/Instar					
	1st	2nd	3rd	4th	5th	Total
Non-parasitized	.58 ± .22	1.76 ± .53	8.11 ± 2.62	40.8 ± 11.94	284.74 ± 48.73	335.96 ± 49.32
Parasitized	.58 ± .22	1.36 ± .38	5.25 ± 1.87	19.86 ± 4.85*	103.16 ± 35.83*	130.79 ± 36.83*

*Significant at the .01 level from non-parasitized larvae.

samples the average white oak was 48.4 cm^2 ± 7.7 cm^2 and the average red oak leaf was 64.8 cm^2 ± 16.2 cm^2. In these studies the "average" larva consumed 5.16 red oak or 6.91 white oak leaves. By taking branch samples from various areas of the canopy it is possible to determine the relative density of larvae per leaf. If early instar densities average 1 larva/10 leaves one would expect approximately 50% defoliation whereas if densities were 1 larva/5 leaves one would expect approximately 100% defoliation. Branch samples taken during mid-August should be used to predict defoliation. The mean larval instar during this time from past studies was ca. 3. If larval densities are greater than 1 per 10 leaves one would expect noticeable defoliation. The "average" oak leaf will vary between sites and years. When predicting defoliation the "average" leaf for each tree species should be assessed for each location.

In 1974, ca. 40% of the larval population was parasitized by D. bethunei. High parasitism levels reduce the expected degree of defoliation. Larvae parasitized by D. bethunei consume ca. 60% less foliage than normal larvae. Thus if parasitism levels were 40% one would expect a 40 x .6 = 24% reduction in expected defoliation.

Control Philosophy and Insecticide Trials

This insect is considered a recreational and urban rather than forest pest. Control of vast acreages of forest land is not warranted because the insect has little impact on

the trees and defoliation rarely lasts more than 1 year. In Michigan, consecutive defoliation does not occur because of large numbers of prepupae remaining in prolonged diapause and a complex of parasitoids and predators attacking the egg and larval populations. The insect has not caused consecutive defoliations in other regions of the U.S. as well, with little tree mortality ever reported.

A large scale spray operation may in fact perpetuate continuous defoliation. In any year a relatively large portion of the population remains in prolonged diapause in the soil. This reservoir population is considered non-susceptible to foliar application of insecticides because prepupae do not feed and are buried ca. 8 cm into the soil and litter. By contrast, most predator and parasitoid populations will be reduced by insecticide application. The reduction would result from: 1) direct insecticide mortality, 2) reduction of host populations and 3) possible reduction of alternate hosts.

Widespread application of insecticides will therefore create a situation in which a large reservoir population emerges in the year following spray application with few natural controlling agents to supress this population. At Big Star Lake in 1974 ca. 2.5 prepupae/.25m^2 remained in the litter and soil. This population was sufficient to again initiate defoliation, particularly if predator and parasitoid populations were reduced by spraying.

In areas where human interaction and usage of oak forests are intense i.e. urban areas, cottage sites, heavy use recreational sites, and along roadsides, spraying may be

justified. Individual home and cottage owners, and resort owners require some form of control to protect their property from defoliation and large numbers of larvae. The acreages involved in spray programs of this type will be small when compared to the overall extent of the defoliation. Consequently, in years subsequent to application of insecticides predators and parasitoids may disperse into sprayed areas from adjacent nonsprayed areas.

At the present time, no insecticides are registered for control of the variable oakleaf caterpillar. In 1974 several insecticides were evaluated for control. The insecticides tested and rates of application are listed in Table 25.

Table 25. Insecticides and dosages applied for control of H. manteo. Michigan, 1974.

Insecticide	Treatment application rates/ 100 gals. water
80% Sevin^{R}W.P.	1.5 lbs.
39% Dylox^{R} L.S.	2 pts.
22.7% Zectran^{R} E.C.	2 pts.
1.3 lb/gal Orthene^{R}	.75 lb/AI
.69% Thuracide^{R} A.S.	2 qts.
3.2% Dipel^{R} W.P.	1 lb.

Each treatment consisted of 3 randomly selected white or red oak trees, 10 to 15 m in height. A Kiekens K.W.H. backpack mist blower was used to apply 1 gal of spray mix per tree. The application was made from atop a 12 m ladder mounted on a 3/4-ton pickup. Three 100 ft^2 polyethylene tarps

were placed beneath trees and phytophagous as well as beneficial insects were collected. Insecticides were applied in the vicinity of Big Star Lake on the morning of 15 Aug, 1974. Temperatures on that date were 25.5°C and wind speed less than 7 km per hour. Insects which dropped to the tarp were collected 24 hours after spray treatment. These were considered the population killed by the insecticide. The mean larval instar during the insecticide trial was 3.2 and no fifth instars were found during spray application. Tarps were left in place beneath the trees and 7 days after spray application a 0.5% spray (pyrethrum) was applied to the canopy of each treatment and surviving organisms were collected and counted. The percent survival was determined by the number of larvae collected from the pyrethrum samples divided by the total number of larvae collected from each tree. The results of insecticides trials are presented in Table 26.

Insecticide trials did not show significant difference between treatments. This was a consequence of poor experimental design (too few samples) and extremely high inter-tree variability of populations. The tests did indicate that a number of compounds proved satisfactory in reducing H. manteo populations. These included Sevin®, Orthene®, and Zectran®. The use of pyrethrum is also suggested for control of larvae because of low mammalian toxicity and excellent efficacy in removing larvae from trees. The effect of insecticides tested on non-target organisms was reported by Wallner and Surgeoner (1974).

To adequately test the efficacy of insecticides two

prerequisites are required: 1) populations sufficient to cause defoliation, and 2) because of high variability approximately 20 trees samples for each insecticide tested. In 1975, populations of H. manteo were too low to adequately evaluate insecticides.

Table 26. Efficacy of insecticides tested for control of H. manteo.

Treatment	Mean No. of Larvae Surviving/Tarp[1]	% Survival
Thuracide	1.3a	36
Dipel	2.0a	75
Sevin	3.3a	15
Zectran	3.7a	21
Orthene	4.7a	28
Dylox	6.0a	55
Untreated	13.0	97

[1]Column means followed by same letter not significantly different at the .05 level by analysis of covariance.

Suggestions for Further Research

This research study was designed to determine the life history and population dynamics of the variable oakleaf caterpillar. The broad nature of the program suggested many avenues of research which should be investigated to present a comprehensive understanding of the biology of this insect. Due to time constraints and resource limitations, I was not able to investigate many of these research areas. Many questions remain unanswered and are here suggested for further

research. I would hope that in all investigations the researcher would ask "Does this insect and the research suggested warrant expenditure of tax dollars or could the resources be better utilized in the study of some other problem?" The damage caused by the variable oakleaf caterpillar is minimal and research should not be related to economic damage. The population dynamics of this insect are similar to many forest and agricultural pests which remain at low densities for long periods of time, yet occasionally produce epidemic populations of short duration. It is hoped that the study of this insect will produce principles of insect population dynamics which can be utilized in the study of other economic pests. For a more comprehensive study of the biology of this insect the following areas of needed research are suggested.

During the 3 years of this study populations of H. manteo have declined since the major defoliation of 1973. We as entomologists and scientists in general become involved in research efforts only when a problem exists. As entomologists we investigate high density rather than low density populations. This investigation has suggested factors which prevent consecutive defoliation and bring about the reduction in population levels. The factors which led to the 1973 defoliation were not studied. This would require a long term research project of populations at low densities. The researcher is presented with major problems in sampling and funding support when studying low density populations. The insect should be viewed as an ideal research organism in the study of insect

population dynamics. The accessibility of the research area, sampling techniques devised during this study, and information concerning population levels in 1973-76 should aid in any future research efforts. A study of the insect at low densities should be attempted. At the very least each August and September prepupal samples could be taken to monitor the prepupal population which remains in prolonged diapause and the overwintering population each year. This population monitoring will indicate when populations again begin to increase and if the percentage prepupae remaining in diapause changes dramatically in any year.

Prepupae provide an excellent research organism for the study of insect diapause. They exhibit: 1) prolonged diapause lasting 1, 2, 3 years and perhaps longer, 2) are relatively abundant and easy to sample, 3) are large and can be readily handled and stored, and 4) laboratory rearing procedures have been developed.

The following questions may be answered in future research:

1. How to differentiate between the various aged prepupae. Some chemical waste product, i.e. uric acid may increase in prepupae as they remain in the soil. This chemical may be identified and quantified to determine age of prepupae.
2. What environmental factors initiate diapause in prepupae.
3. What environmental factors terminate diapause and why do some pupate and others remain in diapause.
4. What environmental factors prevent pupation of prepupae from the first of August to October when soil temperatures

are above the developmental threshold.

The prepupae parasitized by D. bethunei are apparent due to their reduced body and head capsule size. The parasitoid is able to remain in prolonged diapause. Because the prepupae parasitized by D. bethunei are readily identifiable there exists an excellent opportunity to study how the synchronization of diapause between parasitoid and host is accomplished.

Other research objectives should include:

1. Specific identification of egg parasitoids Telenomus sp. and Trichogramma sp. and larval parasitoid Phobocampe sp.
2. Identification of alternate hosts of the insect parasitoids and predators; particularly those on which egg parasitoids overwinter.
3. Factors either intrinsic or extrinsic which affect larval and pupal coloration and the possible use of prepupal color intensity as an indicator of prepupal age.

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APPENDIX

Determination of Larval Instars of *Heterocampa manteo*[1] and Reduction of Larval Head Capsule Size by the Parasitoid *Diradops bethunei*[2,3]

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ABSTRACT

Head capsule measurements were used to distinguish the 5 larval stages of the variable oak leaf caterpillar *Heterocampa manteo* (Doubleday). Parasitization of *H. manteo* larvae by the ichneumonid *Diradops bethunei* (Cresson) resulted in a reduction of head capsule size. Percentage parasitism of overwintering prepupae of *H. manteo* was accurately determined by head capsule measurements.

The variable oak leaf caterpillar, *Heterocampa manteo* (Doubleday), is a late summer defoliator of numerous deciduous trees found throughout eastern United States and Canada (Packard 1895, Wilson 1961). Outbreaks of *H. manteo* seldom last longer than 2 to 3 years. Because parasitism contributes to this population decline, accurate determination of prepupal mortality is essential in formulating population studies and control strategies.

Head capsule measurements have been used to determine the number of instars of various Lepidoptera (Dyar 1890). Utilizing this method Allen and Grimble (1970) reported that the saddled prominent, *Heterocampa guttivitta* (Walker), had 5 larval instars. Packard (1895) presented detailed descriptions of the 5 larval instars of *H. manteo* but did not give accurate head capsule measurements. We found Packard's descriptions unreliable for determining instars of *H. manteo* in Michigan. Here we present an accurate means of determining the instars of *H. manteo* by head capsule measurement and the level of parasitism of *H. manteo* prepupae by *Diradops bethunei* (Cresson) without larval rearing or dissection.

MATERIALS AND METHODS

Larvae of *H. manteo* were collected in Michigan from mixed oak trees July–September 1973. Overwintering prepupae were collected by sifting samples of litter.

RESULTS

Head capsule measurements of 200 larvae of each instar confirmed the presence of 5 instars (Fig. 1). These measurements agreed closely with those determined by Allen and Grimble (1970) for *H. guttivitta* but were less than those given for *H. manteo* by Dyar (1893). He reported head capsule measurements between 4.0 and 4.3 mm for 5th instars, whereas we found them to be between 3.0 and 3.5 mm . An accurate comparison between our study and Dyar's is difficult since he measured only the 5th instar and did not specify how many specimens were examined. Our head capsule measurements were made from one ocellus to the other; however, even at the widest point, the head capsule did not reach 4.0 mm. Differences may be ascribed to geographic variation of the population, the quantity and quality of nutrition, genetic variation or other possible factors.

Head capsule widths of the first 3 instars did not overlap but ca. 20% of the 4th and 5th instars had head capsules smaller than anticipated. Dissection revealed that larvae with the smaller head capsule contained an ichneumonid larva. While there was some overlap between normal and parasitized 4th instar head capsules, parasitized 5th instars exhibited distinctly different widths (Fig. 1). This could lead to some confusion in determining the number of larval instars. The ichneumonid *Olesicampe* sp. nr. *nematorum* (Tshek) caused a similar reduction in the larch sawfly, *Pristiphora erichsonii* (Hartig) (Muldrew 1967).

The parasitoid larvae affecting head capsule size were determined as *D. bethunei*. It was never reared from larvae with normal-sized head capsules and was always reared from larvae possessing the reduced head capsules. Rates of parasitism were 17% in 1973 when *H. manteo* prepupal density was 8.3/0.25 m², and 40% in 1974 when prepupal density was 5.6/0.25 m². The following species of parasitoids were reared from 5th instars of *H. manteo* having normal head capsule size: *Protomicroplitis shisurae* (Muesbeck) (Hymenoptera:Braconidae), *Phobocampe* sp., *Barylypa* sp. (Hymenoptera:Ichneumonidae), *Winthemia datanae* (Townsend), *Lespesia shisurae* (Townsend) and *Archytas aterrimus* (Rob.-Desv.) (Diptera:Tachinidae). Only *Barylypa* sp., *L. shisu-*

[1] Lepidoptera: Notodontidae.
[2] Hymenoptera: Ichneumonidae.
[3] Michigan Agric. Exp. Stn. Journal Article Number 7227.
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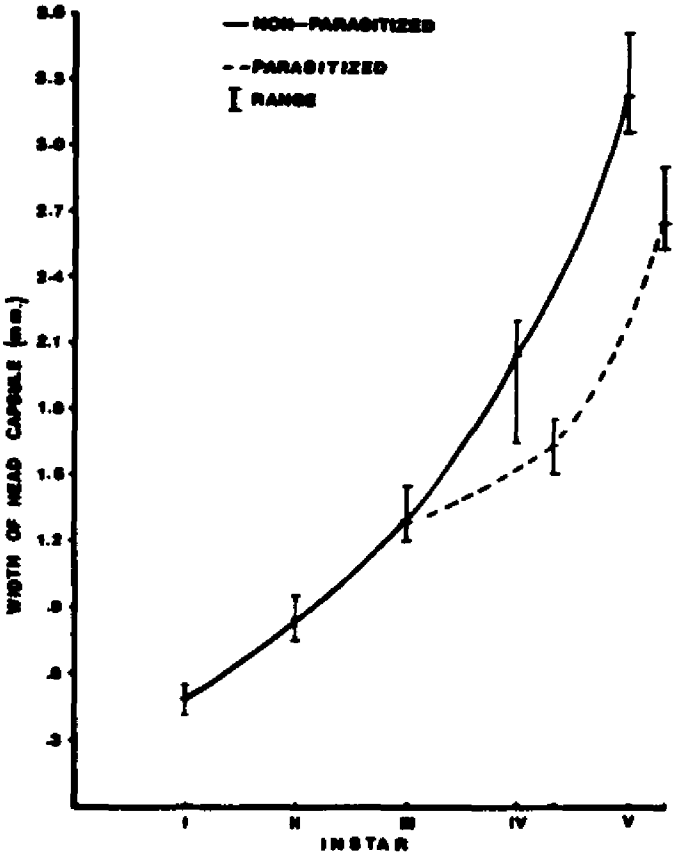

FIG. 1.—Reduction of head capsule size of *H. manteo* by the parasitoid *Diradops bethunei*.

rae and *A. aterrimus* overwintered in *H. manteo* prepupae and had a combined parasitism rate of less than 10%.

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