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ASPECTS OF THE TEMPORAL AND SPATIAL COINCIDENCE OF THE WHITE APPLE LEAFHOPPER (<u>TYPHLOCYBA</u> <u>POMARIA</u> McATEE. CICADELLIDAE. HOMOPTERA) AND TWO PARASITIC HYMENOPTERA

presented by

Hossain Seyedoleslami Esfahani

has been accepted towards fulfillment of the requirements for

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By

#### Hossain Seyedoleslami Esfahani

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## A DISSERTATION

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Hossain Seyedoleslami Esfahani

A descriptive survey was conducted on the temporal and spatial distribution of the white apple leafhopper (WALH), <u>Typhlocyba pomaria</u> McAtee, and two of its parasitoid natural enemies in Michigan apple orchards. A mymarid egg parasitoid, <u>Anagrus epos</u> Girault, and a dryinid nymphal-adult parasitoid, <u>Aphelopus typhlocyba</u> Muesebeck, were found to be the most common natural enemies of the WALH in abandoned apple orchards. They also were the only species which occurred in commercial apple blocks. These two species were considered to be the most promising native natural enemies of the WALH occurring in Michigan for use in current integrated pest management programs.

Based on this survey, WALH egg development, hatch and adult activity and egg parasitoid emergence and activity, on both a calendar and physiological time scale (base temperature 48° F), were estimated. Emergence of <u>An. epos</u> was well synchronized with the availability of WALH eggs. Data are also given indicating that

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Ap. typhlocyba is also well adapted to the occurrence of the nymphal stages of the WALH.

The data described in the previous paragraph, when organized on a physiological time scale, provide a generalized timing model for WALH IPM which can be used to determine sample and spray timing for different stages and generations of the WALH. Based on this model, it is recommended that a delay in spray application until WALH nymphal emergence is complete, is useful if conservation of natural enemies is to be maximal. When high populations of the WALH are expected, or chemical spray programs against other pests are necessary, a delay in spray application may not be realistic. Other alternative strategies for managing the WALH life system are discussed.

Even though the egg parasitoid <u>An.epos</u> is well synchronized to both generations of its host, it is more efficient in parasitising overwintering eggs of the WALH rather than summer eggs. Reasons for this phenomenon are discussed. The higher rate of parasitism of overwintering population is believed to be a result of the close temporal synchrony, spatial coincidence, and density-dependent response of the parasitoid to its host during a period when pesticides are not used. This period provided an excellent biological window for manipulating the parasitoid population. In addition, dispersal of the egg parasitoid from alternative hosts to overwintering WALH populations may increase the efficiency of the egg parasitoid. Dispersal is discussed relative to the population of <u>An.epos</u> emerging from grape leafhopper eggs and attacking the WALH on apple.

## Hossain Seyedoleslami Esfahani

Overwintering eggs of the WALH differed in their distribution on branches, between the upper and lower tree regions, and also among the four cardinal directions within the tree. The major source of variation was between trees. Other sources of variation were attributed to variable management practices used in the orchards studied. The egg parasitoid closely followed distribution of its host relative to this variation in host distribution. The significance of these data relative to sampling programs for the WALH and its parasitoids is discussed.

To Nafiseh and Mariam.

#### ACKNOWLEDGMENTS

I sincerely appreciate the guidance and encouragement given me throughout this study by Dr. Croft, my eajor professor: I am very proud to have been one of his students. Also, I extend appreciation to my guidance committee--Dr. James Bath, Dr. E. D. Klos, Dr. Fred Stehr, and Dr. Oscar Tabonda--for their guidance and suggestions.

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I also appreciate Dr. J. Brunner's helpful comments and Mr. Dave Miller's assistance in data processing through computer programs. Finally, I thank the apple growers in Michigan who cooperated with me during the course of this study.

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 PHENOLOGY OF THE WALH AND ITS EGG AND NYMPHAL-ADVET PARASITOLD RELATIVE TO ENVIRONMENTAL

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			Page
LIST OF	TABLES		vii
LIST OF	FIGURES . Summetions by the WALH		xi
INTRODUC	TIONS Light for of Minimum Thermal Threshold	-	89
	Phenology of the WALR in Relation to Environmenta Temperature		92
Section			
Ι.	LITERATURE REVIEW		5
	Introduction	•••••	5 5 5
	Damage and Host Plants	;	6 6 0
	Associated Species of Leafhoppers in Apple Orchards The Present Status	:	13 13
II.	SEASONAL DISTRIBUTION AND SYNCHRONIZATION OF THE WHITE APPLE LEAFHOPPER AND ITS EGG AND NYMPHAL- ADULT PARASITOIDS		15
	Description of Study Orchards		15
	Enemies and Associated Leafhoppers		17
	Sampling of Overwintening WALH Eggs	•	19
	Sampling of WALH Adults	•	21
	Sampling of Summer WALH Eggs	:	22
	Result and Discussion		24
	Overwintering Eggs		24
	Nymph Activity	•	31
	ACTIVITY OF WALH Adults	•	33
	Fog Parasitoid of the WALH		64
	Nymphal-Adult Parasitoid of the WALH		74
	Conclusion		75

Page

## Section

III.	PHENOLOGY OF THE WALH AND ITS EGG AND NYMPHAL- ADULT PARASITOID RELATIVE TO ENVIRONMENTAL TEMPERATURE	81
	Material and Methods	81 81 85
	Mu Phenology of Parasitoids in Relation to Degree Day Summations by the WALH Result and Discussion Estimation of Minimum Thermal Threshold	87 88 88
	Temperature	92 98
IV.	SPATIAL DISTRIBUTION OF OVERWINTERING AND SUMMER EGGS OF THE WALH AND THE COINCIDENCE OF PARASITISM BY	100
	AN. EPOS TO THE DISTRIBUTION OF ITS HOST	106
	Material and Methods	106
	Parasitism by <u>An. epos</u> Inter- and Intratree Distribution of WALH Eggs	106
	and Coincidence of Parasitism by <u>An</u> , <u>epos</u> Result and Discussion	108 109
	Parasitism by <u>An. epos</u>	109
	and Coincidence of Parasitism by <u>An</u> . <u>epos</u> Conclusion	116 133
۷.	SUMMARY FOR MANAGEMENT RECOMMENDATIONS AND FUTURE RESEARCH	138
	Introduction	138 138 144
	the WALH	145

## Section

LITER	ATURE CITED	148
APPEN	. BIONOMICS OF FOUR SPECIES OF APPLE LEAFHOPPER	152
В	. RAW DATA ON SPATIAL DISTRIBUTION OF OVERWINTERING AND SUMMER EGGS OF THE WALH	174
	Total Neekly Catch and & Accumulation of <u>I. pomaria</u> Adults for Each Generation, Captured on Tellow Traps in Orchard 1, 1975	36
	Mean Number Adult <u>1</u> . <u>pomoria</u> and Total Parasitized Adult <u>1</u> . <u>pomaria</u> Captured on Yellow Trups in Orchard 1. 1976	
	Total Neekly Catch and % Accumulation of T. penarta Adults for Each Generation, Captured on Testing Topos in Onchard 1, 1976	
	Rean Number Adult T. pomaria and Total Receptories Adult T. pomaria Captured on Tailow Crass in Orchard 2, 1976	
	Total Meekly Catch and & Accumulation of 1. Meekly Adults for Each Generation, September 2015 Traps in Orchard 2, 1975	
	Mean Number Adult T. pomarte and the state of the state o	

Page

Traps in	Orchard LIST OF TABLES	

Table		Page
1.	Seasonal Development of Overwintering Eggs of <u>T. pomaria</u> in Orchard 1, 1976	25
2.	Seasonal Development of Overwintering Eggs of <u>I</u> . <u>pomaria</u> in Orchard 2, 1976	26
3.	Seasonal Development of Overwintering Eggs of <u>T. pomaria</u> in Orchard 3, 1976	27
4.	Seasonal Development of Overwintering Eggs of <u>T. pomaria</u> in Orchard 3, 1977	28
5.	Emergence and Development of First Generation Nymphs of the <u>T. pomaria</u> in Orchard 1, 1974	32
6.	Mean Number Adult <u>T. pomaria</u> and Total Parasitised Adult <u>T. pomaria</u> Captured on Yellow Traps in Orchard 1, 1975	34
7.	Total Weekly Catch and % Accumulation of <u>I. pomaria</u> Adults for Each Generation, Captured on Yellow Traps in Orchard 1, 1975	36
8.	Mean Number Adult <u>T</u> . <u>pomaria</u> and Total Parasitised Adult <u>T. pomaria</u> Captured on Yellow Traps in Orchard 1, T976	38
9.	Total Weekly Catch and % Accumulation of <u>T</u> . <u>pomaria</u> Adults for Each Generation, Captured on Yellow Traps in Orchard 1, 1976	40
10.	Mean Number Adult <u>T</u> . <u>pomaria</u> and Total Parasitised Adult <u>T</u> . <u>pomaria</u> Captured on Yellow Traps in Orchard 2, 1976	42
11.	Total Weekly Catch and % Accumulation of <u>T. pomaria</u> Adults for Each Generation, Captured on Yellow Traps in Orchard 2, 1976	44
12.	Mean Number Adult I. pomaria and Total Parasitised Adult I. pomaria Captured on Yellow Traps in Orchard 3, 1976 .	46

## Table

13.	Total Weekly Catch and % Accumulation of <u>T</u> . <u>pomaria</u> Adults for Each Generation, Captured on Yellow Traps in Orchard 3, 1976	48
14.	Seasonal Distribution of First Generation Eggs of <u>I. pomaria</u> in Orchard 1, 1975	52
15.	Seasonal Distribution of First Generation Eggs of <u>I. pomaria</u> in Orchard 1, 1976	53
16.	Comparison of Two Egg Detecting Techniques for Summer Eggs of <u>T</u> . <u>pomaria</u> , Through Time	61
17.	Distribution of Summer Eggs of <u>T</u> . <u>pomaria</u> in Four Different Zones of Apple Leaves	62
18.	Development of <u>A</u> . <u>epos</u> in Overwintering Eggs of <u>T</u> . <u>pomaria</u> in Orchard 1, 1976	65
19.	Development of <u>A</u> . <u>epos</u> in Overwintering Eggs of <u>T</u> . <u>pomaria</u> in Orchard 2, 1976	66
20.	Development of <u>A. epos</u> in Overwintering Eggs of <u>T. pomaria</u> in Orchard 3, 1976	67
21.	Egg Parasitoids Reared From Three Species of Leafhoppers in Michigan Apple Orchards	71
22.	Comparison of Mortality and Rate of Parasitism by A. epos on Overwintering Eggs of the White Apple	72
23.	Source of Weather Data Used for Correlation of	13
	Phenology of <u>T</u> . <u>pomaria</u> to Environmental Temperature	83
24.	Degree Day Summation From January 1 for 2% and 50% Development and Activity of Different Stages of the L. pomaria	97
	Traps in Orchard 1, 3976	"
25.	Degree Day Summations Above 48° F From January 1 Relative to Activity of <u>A</u> . epos (Part A) and <u>A</u> . typhlocyba (Part B)	99
26.	Mean Density Differences of <u>T. pomaria</u> Overwintering Population for 72 5-cm Lengths of Each 1-5 Growing Season Old BranchesOrchard 1, 1974	110

Table

-				
	-	~	-	
$\mathbf{r}$	-		~	
	u	-	~	

27.	Mean Density Differences of <u>T. pomaria</u> Overwintering Population Relative to Distance From Apical Part of the Branch, 1976	114
28.	Mean, Variance, and Coefficient of Negative Binomial (k value) Statistical Parameters for Overwintering	
	by <u>A. epos</u> in Orchards 1, <u>2</u> , and 3, 1976	118
29.	Analysis of Variance of Inter- and Intratree Variability in Overwintering Eggs of <u>I</u> . <u>pomaria</u> , Orchard 1, 1976	122
30.	Analysis of Variance of Inter- and Intratree Variability in Parasitised Overwintering Eggs of <u>T</u> . <u>pomaria</u> by <u>A</u> . <u>epos</u> , Orchard 1, 1976	122
31.	Analysis of Variance of Inter- and Intratree Variability in Overwintering Eggs of <u>I</u> . pomaria, Orchard 2, 1976 .	124
32.	Analysis of Variance of Inter- and Intratree Variability in Parasitised Overwintering Eggs of <u>T</u> . <u>pomaria</u> by <u>A</u> . <u>epos</u> , Orchard 2, 1976	124
33.	Analysis of Variance of Inter- and Intratree Variability in Overwintering Eggs of <u>T</u> . pomaria, Orchard 3, 1976	127
34.	Analysis of Variance of Inter- and Intratree Variability in Parasitised Overwintering Eggs of <u>T</u> . <u>pomaria</u> by <u>A</u> . <u>epos</u> , Orchard 3, 1976	127
35.	Distribution of Overwintering Eggs of <u>E</u> . <u>maligna</u> on Apple Branches in Relation to Distance From Apical Part of the Branch, 1976	154
36.	Total Number of Adult <u>E. maligna</u> Captured on 12 Yellow Traps in Orchard 1, 1975	155
37.	Total Number of Adult E. maligna Captured on 12 Yellow Traps in Orchard 1, 1976	156
38.	Total Number of E. <u>maligna</u> Captured on 6 Yellow Traps in Orchard 2, 1976	156
39.	Change in Population Density of Overwintering Eggs of <u>T. pomaria</u> and <u>E. maligna</u> in Two Apple Plots in Orchard 1, Through 3 Continuous Years	161

Table

40.	Total Counts of Table 39 Weighted for 325 Leaf Clusters for Each Year in Each Plot	162
41.	Total Number of Adult <u>E. fabae</u> Captured on 12 Yellow Traps in Orchard 1, 1975	164
42.	Total Number of Adult <u>E. fabae</u> Captured on 12 Yellow Traps in Orchard 1, 1976	166
43.	Total Number of Adult <u>E</u> . <u>lawsoniana</u> and Total Parasitised Adult <u>E</u> . <u>lawsoniana</u> Captured on <u>12</u> Yellow Traps in Orchard <u>1.</u> <u>1975</u>	167
44.	Total Number of Adult E. <u>lawsoniana</u> and Total Parasitised Adult <u>E. lawsoniana</u> Captured on 12 Yellow Traps in 975 Orchard 1, 1976	169
45	Total Number of Adult F. lawsoniana and Total Parasitised	
40.	Adult E. lawsoniana Captured on 6 Yellow Traps in	
	Orchard 2, 1976	1/1
46.	Raw Data on Inter- and Intratree Distribution of Overwintering Eggs of the <u>T</u> . <u>pomaria</u> and Parasitised Eggs by <u>A</u> . <u>epos</u> , Orchard 1, 6/19/74	174
47.	Raw Data on Inter- and Intratree Distribution of Overwintering Eggs of T. <u>pomaria</u> and Its Mortality Factors, Orchard 1, 1976	175
48.	Raw Data on Inter- and Intratree Distribution of	
	Overwintering Eggs of <u>T</u> . <u>pomaria</u> and Its Mortality Factors, Orchard 2, 1976	178
49.	Raw Data on Inter- and Intratree Distribution of Overwintering Eggs of T. <u>pomaria</u> and Its Mortality Factors, Orchard 3, 1976	181
50.	Raw Data on Inter- and Intratree Distribution of Summer Eggs of <u>I</u> . <u>pomaria</u> , Wasem Orchard, 8/13/77	184
	Seasonal Distribution of Three Spectra of Las Property,	

 Seasonal Distribution of The Eggs Laid in Leaf Tissue, To pomaria, Orchard 1, 197

# LIST OF FIGURES

Figure		Page	ł
11.	Seasonal Development (A) and Hatch (B) of Overwintering Eggs of <u>T</u> . pomaria, 1976-1977	29	,
2.	Seasonal Distribution of Adult <u>T. pomaria</u> and Its Parasitised Numbers by <u>A. typhlocyba</u> in Orchard 1,1975	. 35	5
3.	Cumulative Percentage Trap Catch <u>T. pomaria</u> for Males and Females Together and Separately in Orchard 1, 1975	. 37	,
4.	Seasonal Distribution of Adult <u>T. pomaria</u> and Its Parasitised Numbers by <u>A. typhlocyba</u> in Orchard 1,1976	. 39	,
5.	Cumulative Percentage Trap Catch <u>T. pomaria</u> for Males and Females Together and Separately in Orchard 1, 1976	. 41	
6.	Seasonal Distribution of Adult <u>T. pomaria</u> and Its Parasitised Numbers by <u>A. typhlocyba</u> in Orchard 2, 1976	. 43	5
7.	Cumulative Percentage Trap Catch <u>T. pomaria</u> for Males and Females Together and Separately in Orchard 2, 1976	. 45	
8.	Seasonal Distribution of Adult <u>T. pomaria</u> and Its Parasitised Numbers by <u>A. typhlocyba</u> in Orchard 3, 1976	. 47	
9.	Cumulative Percentage Trap Catch <u>T. pomaria</u> for Males and Females Together and Separately in Orchard 3, 1976	. 49	
10.	The Degree of Precision With Which the Mean T. pomaria Trap Catch is Defined for 12 Traps	. 55	
11.	The Degree of Precision With Which the Mean <u>T</u> . <u>pomaria</u> Trap Catch is Defined for Six Traps	. 56	
12.	Seasonal Distribution of Three Species of Leafhoppers, Eggs Laid in Leaf Tissue, and Oviposition Trend of <u>T. pomaria</u> , Orchard 1, 1975	. 59	Source and the
13. 26.	Seasonal Distribution of Three Species of Leafhoppers, Eggs Laid in Leaf Tissue, and Oviposition Trend of <u>I. pomaria</u> , Orchard 1, 1976	. 60	

## Figure

14.	Development of <u>A</u> . <u>epos</u> on Overwintering Eggs of <u>T</u> . <u>pomaria</u>		69
15.	Coefficient of Variation in Degree Days at Various Base Temperatures for <u>T</u> . <u>pomaria</u> Overwintering Egg Development, Orchards 1, 2, 3, 1976		89
16.	Coefficient of Variation in Degree Days at Various Base Temperatures for $\underline{T}. \ \underline{pomaria}$ Nymph Maturation .		90
17.	Approximation of Base Temperature for <u>T</u> . <u>pomaria</u> Nymph Maturation		91
18.	Correlation of Overwintering Egg Development and Hatch of $\underline{T}$ . pomaria to Degree Days Summations		93
19.	$\begin{array}{llllllllllllllllllllllllllllllllllll$		94
20.	Average Regression Lines for Probit Transformed Data for Egg Development Hatch, Male and Female Activity of <u>I</u> . pomaria		95
21.	Phenology of <u>T</u> . <u>pomaria</u> in Relation to Degree Day Summation		96
22.	Mean Density Differences of <u>T. pomaria</u> Overwintering Population for 72 5-cm Lengths of Each 1-5 Growing Seasons Old Branches, Orchard 1, 1974		111
23.	Distribution of Proportion of Total Eggs and Parasitised Eggs of <u>T. pomaria</u> Overwintering Population on 1-5 Growing Seasons Old Branches, Orchard 1, 1974		112
24.	Mean Density Differences of <u>T. pomaria</u> Overwintering Population Relative to Distance from Apical Part of the Branch (A) and Degree of Precision That Describes These Differences (B)		115
25.	Distribution of Proportion of Total Eggs and Parasitised Eggs of <u>I. pomaria</u> Overwintering Population in Different Sampling Sites, Orchard 1, 1974.		117
26.	Fitting of Negative Binomial to Observed Distribution of Overwintering Eggs of <u>I</u> . pomaria and Parasitised Eggs by A. epos. orchard <u>3</u> . 1976		119

Figure Page

27.	Distribution of Proportion of Total Eggs and Parasitised Eggs of Overwintering <u>T. pomaria</u> Population in Different Sampling Sites in Orchard 1, 1976	123
28.	Distribution of Proportion of Total Eggs and Parasitised Eggs of Overwintering <u>T</u> . <u>pomaria</u> Population in Different Sampling Sites in Orchard 2, 1976	125
29.	Distribution of Proportion of Total Eggs and Parasitised Eggs of Overwintering <u>T. pomaria</u> Population in Different Sampling Sites in Orchard <u>3</u> , 1976	128
30.	Response of <u>A</u> . <u>epos</u> to Aggregation of Overwintering Eggs of <u>T</u> . <u>pomaria</u> in Orchard 1, 1976	130
31.	Response of <u>A</u> . <u>epos</u> to Aggregation of Overwintering Eggs of <u>T</u> . <u>pomaria</u> in Orchard 2, 1976	131
32.	Response of <u>A</u> . <u>epos</u> to Aggregation of Overwintering Eggs of <u>T</u> . <u>pomaria</u> in Orchard 3, 1976	132
33.	Distribution of Proportion for Summer Eggs of <u>T. pomaria</u> in Different Sampling Sites in Wasem Orchard, 1977	134
34.	Seasonal Distribution of Adult <u>E</u> . <u>maligna</u> , Orchard 1, 1975	157
35.	Seasonal Distribution of Adult Male and Female <u>E. maligna</u> and Its Eggs, Orchard 1, 1976	158
36.	Seasonal Distribution of Adult <u>E</u> . <u>fabae</u> , Orchard 1, 1975 and 1976	165
37.	Seasonal Distribution of Adult <u>E</u> . <u>lawsoniana</u> , Orchard 1, 1975	168
38.	Seasonal Distribution of Adult <u>E</u> . <u>lawsoniana</u> , Orchard 1, 1976	170
39.	Seasonal Distribution of Adult <u>E</u> . <u>lawsoniana</u> , Orchard 2, 1976	172

the U.S. continued to intensify, especially in recent years (Trumme) 1974: Howitt.<sup>1</sup> unpublished data).

Research on control of INTRODUCTION: a last decade has almost

The white apple leafhopper (WALH) is distributed throughout the United States (Metcalf, 1968), but most frequently is a problem on apples in the northern temperate regions of the fruit belt (Ackerman & Isely, 1931). In spite of its status as a pest from time to time, the WALH is much less frequently observed in unsprayed orchards in these regions. This is probably a result of two factors, less tree vigor and the biological control impact of natural enemies. In fact, Garman and Townsend (1936) stated that ". . . so successful is the natural control of the white apple leafhopper in Connecticut that unsprayed trees are rarely, if ever seriously harmed" by this species.

In the first few years following the introduction of DDT for apple pest control, the WALH was of little consequence as a pest. Thereafter, it developed resistance to this compound (Glass, 1960), as did several other fruit pest species, and control failures for the WALH increased where this compound continued in use. Many growers switched from DDT and began using organophosphorous-related (0-P) compounds such as parathion and azynophosmethyl for broad-spectrum insect control. Thereafter, the WALH acquired resistance to these compounds (Trammel, 1974) and as a consequence, their pest status in commercial apple orchards of the midwestern and northern regions of

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the U.S. continued to intensify, especially in recent years (Trammel, 1974; Howitt, <sup>1</sup> unpublished data).

Research on control of the WALH in the last decade has almost exclusively been based on chemical control measures (Trammel, 1974; Asquith et al., 1975; Hull & Asquith, 1978; Reissig et al., 1978; Weires & Smith, 1978). While this research is important, unilateral chemical applications should only be viewed as an intermediate remedy since developed resistance, pest resurgence, increased pesticide costs, and continued environmental concerns will likely limit their long-term use. Integrated pest management (IPM) (Glass, 1975) seems to be a more appropriate control strategy for this pest. Such an approach would fit well into the already on-going, on-line IPM system established by Croft and co-workers for Michigan orchards. To date, programs for the European red mite (Croft, 1975), the codling moth (Ried] & Croft, 1978), green apple aphid (Jokinen & Croft, personal communication<sup>2</sup>), and a variety of other species (Welch et al., 1978) are in progress. Continued research and new species IPM systems are needed, because the pest status of these species is continually changing and new IPM and crop production technologies usually affect each other. research was to estimate

For the WALH, both of these rationale apply. The changing pest status of this insect was mentioned above. Relative to control

<sup>&</sup>lt;sup>1</sup>Angus J. Howitt, Department of Entomology, Michigan State University, East Lansing, Michigan.

<sup>&</sup>lt;sup>2</sup>D. Jokinen and B. A. Croft, Department of Entomology, Michigan State University, East Lansing, Michigan.

system interactions, the WAHL is most often a problem in the second generation. This is often at the same time that biological control of the European red mite, <u>Panonychus ulmi</u> (Kock), is occurring by the predatory mite <u>Amblyseius</u> fallacis (Garman). If chemical control of the WALH is necessary, biological control of the European red mite may be sacrificed since presently there are few chemicals which will control the WALH, but which are selective to the predatory mite, <u>A. fallacis</u> (Croft &McGroarthy, 1977). To find a solution to these problems, more information about the WALH life-system is needed.

Literature on the biology of the WALH is very incomplete and there is no information on Michigan populations. For this reason, a descriptive survey and study of the temporal and spatial distribution of this insect was warranted. Also, since initial observations (Section II) indicated that a mymarid egg parasitoid, <u>Anagrus epos</u> Girault, and a dryinid nymphal-adult parasitoid, <u>Aphelopus typhlocyba</u> Muesebeck, were very common natural enemies in commercial and abandoned orchards, a similar study of their temporal and spatial distribution and coincidence relative to the WALH was in order. This information is the basic topic of this thesis. The overall objective of this research was to estimate the potential for management of this pest-natural enemy system in the field.

Knowledge of the temporal and spatial distribution of an insect is basic to sampling the insect and any type of decision-making process for control of the insect. When dealing with the synchronization and spatial coincidence of a host and its natural enemies,

guidelines for management can be formulated to protect the natural enemies and increase their efficiencies relative to biological control of a pest. Furthermore, study of these relationships may contribute to the theory of biological control. Franz (1964) has stated that "biological control in part is an attempt to establish coincidence between host and its natural enemies."

Study areas in this thesis are dealt with in five separate but related sections and two appendices. Section I is a review of literature. Section II deals with the seasonal distribution of WALH and its two parasitoids. In Section III, data from Sections I and II are incorporated into a phenology model of WALH development in relation to environmental temperature. In Section IV, the spatial distribution of the WALH in the egg stage, the coincidence of parasitism by <u>An</u>. epos and trends of density dependency in this parasitoid are discussed. Section V integrates the previous sections, discusses pest management strategies for the WALH, and indicates future research needs. Information on other leafhoppers commonly associated with the WALH in Michigan apple orchards is listed in the appendix. The bionomics of these species are discussed in Appendix A. Appendix B includes the raw data collected on the spatial distribution of the WALH eggs.

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# LITERATURE REVIEW

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The bionomics of leafhoppers has been reviewed by Delong (1971). Monographs on Homoptera (Metcalf, 1968) give citations of the world leafhoppers. Important taxonomic characters and the taxonomic status of leafhoppers are presented in Delong (1948) and Beirne (1956). This review deals with the literature on economically important leafhoppers occurring on apple and includes the white apple leafhopper (WALH) and other leafhopper species associated with it.

## that high populations The White Apple Leafhopper

# Distribution, Taxonomy, Machine and Morphology

The WALH is native to North America (Ackerman & Isely, 1931), having been reported from Alaska, British Columbia, Saskatchewan, Ontario, and Nova Scotia in Canada (Beirne, 1956) and from most applegrowing areas of the United States (Metcalf, 1968). This insect was described as <u>Typhlocyba pomaria</u> McAtee (McAtee, 1926). The common name "white apple leafhopper" was first proposed by Ackerman and Isely (1931). In American and Canadian literature, the WALH has been confused with the rose leafhopper, <u>Typhlocyba rosae</u> (Linnaeus). Ackerman and Isely (1931) considered that research published on the

rose leafhopper from apple orchards previous to 1926 in fact pertained to the WALH. The taxonomic status of <u>T</u>. <u>pomaria</u> has been reviewed by Beirne (1956) and Metcalf (1968). A full description of the morphology of adults was described by McAtee (1926). Ackerman and Isely (1931) more clearly described morphology of all other stages. The taxonomy and morphology of this species are well known at present; however, several other leafhoppers are associated with WALH in apple orchards. Careful identification of these species is extremely important in the field.

Damage and Host Plants

The WALH is a mesophyl feeder causing mottling of leaves, and excreting honey dew on leaves and fruits. Later, a black fungus will develop on these honey dews. Also, some apple growers claim that high populations of the adult leafhoppers annoy apple pickers. Preferred hosts of the WALH are: apple, <u>Prunus</u> spp, and hawthorn (Beirne, 1956). Different apple varieties show different susceptibility to the WALH. Rhode Island Greening, North Western Greening, Baldwins, Duchess, and Jonathan are more susceptible. Wealthy, McIntosh, Rome Beauty, TwentyOunce, Ben Davis, and Delicious varieties are moderately susceptible. The WALH is scarce on crab apple (Trammel, 1974).

#### Life Cycle ssible to locate eggs prior to locate

The life cycle of the WALH has been studied by Ackerman and Isely (1931), Chapman and Hammer (1932), Armstrong (1936), Garman and Townsend (1936), respectively, in Arkansas, New York, Ontario, and

Connecticut. Hereafter, the work of Armstrong is reviewed in more detail.

Armstrong (1936) reported two generations per year in Ontario. The WALH overwinters in the egg stage, and overwintering eggs are laid in the collenchyma tissue of the cortex under the bark, usually in 2-5 year old shoots. Overwintering eggs in Ontario start hatching during May about the time of cluster buds separation. More than 90% of eggs are hatched during the next 2 weeks. Small nymphs move to the undersurface of leaves and afterwards stay on the same leaf until they develop to adults. Occasionally movement occurs between leaves in the later nymphal instars. This insect has five nymphal stages. The first four exuvia can be removed from the leaves by light breezes and rainfall, but the last nymphal skin tends to remain on the undersurface of leaves for the duration of the growing season. Average nymphal duration was 23 days in 1933 and 27.45 days in 1934. The female preoviposition period averaged 13.4 days in 1933 and 9 days in 1934. The oviposition period varied 7-34 days with an average of 20.6 days. The post-oviposition period varied from 1-26 days and averaged 6.2 days. In cold weather, adults rested under the surface of leaves, but in warm periods they were active. Mated females of the first generation deposited eggs in the undersurface of leaves in the main midrib, larger veins, and petioles. It was impossible to locate eggs prior to hatching, but parasitised eggs were observable since emergence holes of egg parasitoids are visible. Oviposition of the first generation WALH adults started

in June and continued into August. The incubation period of summer eggs varied between 20-64 days, averaging 39 days. Second-generation eggs hatched in the second half of July and continued into September. Average duration of nymphal instars was 22.3 days in 1933 and 23.85 days in 1934 in insectary condition. Adults of the second generation appeared on August 3 under insectary condition, but were not observed until mid-August in the field where they were active until late October.

The life cycle of the WALH has been similarly described by other authors; some variations in different localities have been reported. Chapman and Hammer (1932) observed that emergence of the nymphs from the overwintering eggs did not follow the phenology of the host plant. They did not elaborate on the specific details of this behavior. Ackerman and Isely (1931) reported the incubation period of summer eggs of the WALH varied between 64-86 days, averaging 74.6 days in Arkansas. The authors suspected that high temperature caused this extended incubation period.

#### Control Methods

Natural factors other than natural enemies. The WALH is limited by high temperature. Those above 100° F kill many individuals (Ackerman & Isely, 1931). Population of the WALH will decrease after several successive dry years. On the other hand, rainy seasons kill many nymphs (Garman & Townsend, 1936). Rainy seasons will improve conditions for development of an epidemic disease by Entomophthora sphaerosperma (Shoene, 1938). Low nutritional value

of the host plant expressed as reduced new growth is another factor influencing populations of the WALH. Also, variable susceptibility of different varieties of apple to WALH has been reported (Trammel, 1974).

Natural enemies. Natural enemies have always been considered important mortality factors contributing to the natural control of the WALH. Spiders, the mymarid egg parasitoid, <u>Anagrus armatus</u> Ashmead, and a dryinid nymphal-adult parasitoid, <u>Aphelopus Sp</u>, were reported as important in Connecticut (Garman & Townsend, 1936). Nymphs and adults of the mirid, <u>Hyaliodes vitripennis</u> Say, the egg parasitoids <u>Anagrus armatus</u> var <u>nigriventris</u> Girault and <u>Anagrus</u> <u>epos</u> Girault and a dryinid nymphal-adult parasitoid were noted in Arkansas (Ackerman & Isely, 1931). Spiders, birds, <u>H. vitripennis</u>, <u>Aphelopus Sp</u> near <u>microleucus</u> Perkins and <u>An. armatus</u> have been reported from Ontario (Armstrong, 1935). The mirid predators, <u>Diaphnidia</u> <u>pellucida</u> Uhler and <u>H. vitripennis</u> and egg parasitoid <u>An. armatus</u> and nymphal-adult parasitoids <u>Aphelopus typhlocyba</u> Muesebeck have been observed in New York (Steiner, 1938) and <u>An. epos</u> was reported from British Columbia (McKenzie & Beirne, 1972).

Among these natural enemies the mymarid egg parasitoids and the dryinid nymphal-adult parasitoids have been studied the most. They are generally concluded to be most common and specific natural enemies of the WALH. At present there is little basic research data to suggest if any or a complex of these natural enemies are capable of regulating population of the WALH. However, the previous success

of parasitoids in biological control would cause one to consider them to be more efficient regulators of these pests than predators in general (Huffaker et al., 1976). In addition, during early observations in Michigan apple orchards it was found that the egg parasitoid, <u>An. epos</u>, and the nymphal-adult parasitoid, <u>Ap. typhlocyba</u>, were the only common natural enemies of the WALH in commercial blocks. Present information on the biology of these two groups of natural enemies, their presence in undisturbed orchard habitats, their persistence in orchards exposed to spraying programs, and their general specificity to the host prompted further research on these two groups of natural enemies. Certain behavioral aspects of the biology of these two groups of natural enemies will be discussed relative to their future use in pest management programs for the WALH.

Mymarid egg parasitoids: Two species of parasitoids from this family attack the WALH. The biology of the first species, <u>An.armatus</u>, was reported differently by Armstrong (1935) from Ontario and by Steiner (1938) from New York. In Ontario, adult egg parasitoids emerged from their overwintering sites in synchrony with the oviposition period of the first WALH generation in summer. In New York, they emerged in three different periods of time: (a) during the emergence period of the WALH nymphs from the overwintering eggs, (b) during the oviposition period of the first generation adults, and (c) during the oviposition period of the second generation adults. This parasitoid caused a maximum mortality of 96% on the overwintering eggs of the WALH in New York, but it was less efficient on overwintering

eggs laid on water sprouts and suckers and also less effective on summer eggs. In this regard, Steiner (1938) recommended pruning water sprouts and suckers to decrease pest levels and to change parasite-host ratios. The taxonomic status of the Anagrus armatus group is complex and several subspecies have been reported. Recently, however, a new key to genera of Anagrus in North America has been published, which lumped all these subspecies together as An. armatus Ashmead (Gordh & Dunbar, 1977). The second species is An. epos. This parasitoid in association with An. armatus was reported initially from West Chester, Pennsylvania (Ackerman, 1919). McKenzie and Beirne (1972) reported it as an efficient natural enemy of the grape leafhopper, Erythroneura ziczac Walsh in British Columbia, and noted overwintering eggs of T. pomania as an overwintering refuge for this parasitoid. They observed only two periods of emergence of the adult parasitoid from this overwintering refuge early in the season. Overall, 11 species of leafhoppers are reported as alternative hosts of An.epos (Peck, 1963), but its biology has been more extensively studied on the grape leafhopper Erythroneura elegantula Osborn and Rubus leafhopper, Dikrella curentata (Gillette) by Jensen et al. (1973) and Doutt and Nakata (1973). Later, Cate (1974) reviewed pertinent literature on this species and studied its effect on the dynamics of E. elegantula in California. Also, its biology on plum leafhopper, Typhlocyba prunicola Edward, has been reported from California by Mulla (1956).

Dryinid nymphal-adult parasitoid: Two dryinids are important in this group: Ap. microleucus from Ontario (Armstrong, 1935) and

Ap. typhlocyba from New York (Steiner, 1936, 1938). Although they are treated as two different species (Muesebeck et al., 1951), the biology of each species is similar. The taxonomy of this group is not well known. It is currently under revision by Dr. P. Freytag (personal communication) from the University of Kentucky. These parasitoids overwinter in the larval stage as a cocoon in the soil, and adult parasitoid emergence is synchronized with nymph emergence of the WALH. The female parasitoid oviposits in the abdomen of leafhopper nymphs, but parasitised nymphs show no external symptoms. In the adult stage of the host, a pouch-shaped cyst appears on the abdomen of the leafhopper. Parasitised adult leafhoppers are active except for the last 2 days of life before the larvae of the parasitoid leave the host body. When the larvae of the parasitoid leave the body of the host, the dying leafhopper embeds its tarsi in the leaves and remains on the undersurface of the leaf for the remainder of the season. Parasitoid larvae change to pupa in the soil, and after approximately 40 days adults emerge. Emergence is closely synchronized with the emergence of the second generation nymphs of the WALH.

<u>Chemical control</u>. The history and current status of chemical control recommendations for this pest have been discussed in the introduction. They will not be discussed further here. A detailed review of chemical control of this species in New York is in Trammel (1974).

this species should be developed. A destruction of the second of this insect is necessary before its modernment of a development of the second of the second

## Associated Species of Leafhoppers in Apple Orchards

The association of several additional species of leafhoppers with the WALH has been reported in apple orchards in several localities by different investigators. In Vineland, Ontario, Canada, Typhlocyba pomaria, Empoasca fabae (Harris), Empoasca maligna Walsh. and Typhlocyba rosae were observed. Also Erythroneura lawsoniana Baker was found in small numbers and the grape leafhopper, Erythroneura Comes Say, immigrated into apple orchards in autumn (Armstrong, 1936). In the Ozarks, Arkansas, Erythroneura obliguae (Say), Erythroneura maculata (Gill), E. fabae, E. maligna, and T. pomaria are associated together, but damage is mainly caused by the first two species. Erythroneura hartii Gill, T. rosae, Typhlocyba xanthippe McAtee, and Idjocerus provencheri Vanduzee along with T. pomaria have been reported as occasional apple pests in northern fruit areas (Ackerman & Iselv. 1931). No specific published reports were available on leafhoppers in Michigan apple orchards, until Taboada (1964) published a species list.

## The Present Status

Since it appears that WALH mostly is a pesticides-induced pest of apple and since pesticides will likely be essential in apple orchard management systems for many years to come, an integrated approach using alternative nonpesticidal measures for controlling this species should be developed. A knowledge of the ecology of this insect is necessary before its management can be undertaken; at present these data are not available. Also, the life history of the WALH appears to vary in different geographical areas, and several species of leafhoppers are associated with it, making identification of life stages difficult. Study of these leafhopper species should be undertaken in different localities. Also, there is confusion as to the taxonomic status of the parasitoid complex attacking the WALH. Biological and taxonomic evaluations of these parasitoids should help to clear up these questions.

During the period 1973-77, 36 abandoned, seet-exemptioned, and commercial apple orchards throughout Michigan were station for general observation. Detailed sampling data, homever, were taken in two abandoned and one commercial apple blocks:

Orchard 1 (Nadeou Orchard) 1974-77--This abundance withand is located 15 miles north of Lowell, Kent County, Michigan. It is surrounded by wood Tots on the south and east and is converse by mean fields and rangelands in north and west. It has been emailed since 1971, and includes 129 apple trees of the idealed, Bee Beltthour, McIntosh, and Jonathan varieties. Other wester have been a belt thour, prior to 1971 indicated that the write apple to compare for the series on abundant pest in this orchard. During the analyse of the tively low population of the SALM was product.

Orchand 2 (Kalamazoo State Huspita) washed as a semi-abandoned orchand located in Kalamazoo State Huspita) washed as a semi-abandoned orchand located in Kalamazoo State Huspita) and insecticide tests. An unsprayed

to the west by Michigan Highway 131, in the east by other apple blocks, and on the south and north by open fields was selected for study. This block had 150 appsection II 12 different variation.

SEASONAL DISTRIBUTION AND SYNCHRONIZATION OF THE WHITE APPLE LEAFHOPPER AND ITS EGG AND NYMPHAL-ADULT PARASITOIDS

## Dechards Description of Study Orchards

During the period 1973-77, 36 abandoned, semi-abandoned, and commercial apple orchards throughout Michigan were visited for general observation. Detailed sampling data, however, were taken in two abandoned and one commercial apple blocks:

Orchard 1 (Nadeau Orchard) 1974-77--This abandoned orchard is located 15 miles north of Lowell, Kent County, Michigan. It is surrounded by wood lots on the south and east and is bordered by open fields and rangelands in north and west. It had been abandoned since 1971, and includes 129 apple trees of the Ida-Red, Red Delicious, McIntosh, and Jonathan varieties. Observation taken by the grower prior to 1971 indicated that the white apple leafhopper (WALH) was an abundant pest in this orchard. During the study period, a relatively low population of the WALH was present.

Orchard 2 (Kalamazoo State Hospital Orchard) 1976-77--This is a semi-abandoned orchard located in Kalamazoo County, Michigan. Different blocks in this orchard were used for experimental fungicide and insecticide tests. An unsprayed portion of this orchard bordered
to the west by Michigan Highway 131, in the east by other apple blocks, and on the south and north by open fields was selected for study. This block had 150 apple trees of 12 different varieties. The entire orchard occasionally received fertilizer application, and once a year the ground cover was mowed and the apple trees pruned. Trees sustained good vegetative growth each season, but leaves were damaged by apple scab and leaf defoliators.

Orchard 3 (Graham Agricultural Experiment Station) 1976-77--This commercial apple orchard is located in Kent County, Michigan, and is surrounded on the north by an open field and by a small wood lot. In the south, it is bordered by commercial peach and cherry plantations and by open fields in the west and east. This block received standard cultural management practices; however, the only broadspectrum insecticide applied was azinphosmethyl during 1975-1977. The WALH is generally resistant to this compound. This block contained 138 apple trees, including the varieties Red Delicious, Northern Spy, Vance, Rome, and Jonathan.

Selection of these orchards was made on the basis of their previous management histories and ecological status. Sites 1 and 2 were considered to be representative of an abandoned and semiabandoned orchard in Michigan. It was anticipated that they would reflect the more undisturbed population dynamics of the WALH and its natural enemies. Orchard 3 was selected to reflect a selectively sprayed commercial apple orchard.

### Preliminary Identification of WALH's Natural Enemies and Associated Leafhoppers

Initially, commercial and abandoned apple blocks were visited to observe, collect, and identify the natural enemies of the WALH. Different leafhopper life stages were collected and dissected in the laboratory for parasitoid detection. An unknown egg parasitoid and an unknown adult parasitoid were the most commonly observed species found by this method.

Apple branches containing overwintering eggs of the WALH were collected and maintained in emergence cages made from ice cream cartons containing an observation and collection vial mounted on the carton wall. On branches, other insects and insect residues were removed and WALH eggs were marked and maintained in separate cages. In many cases a mymarid egg parasitoid emerged therefrom. On branches with marked eggs, the number of parasitoids captured often was equal to the number of emergence holes on WALH eggs. All specimens reared in this study were identified by Dr. Gordon Gordh<sup>1</sup> as <u>Anagrus epos</u> Girault from the family Mymaridae.

Nymphal-adult parasitoids were reared similarly in cages partially filled with sterilized soil and on uninfested apple branches. Adult WALH's parasitised by this species were collected and released in these cages. Emerged specimens were identified by Dr. P. Freytag<sup>2</sup> as <u>Aphelopus typhlocyba</u> Muesebeck from the family Dryinidae.

<sup>&</sup>lt;sup>1</sup>G. Gordh, Department of Entomology, University of California/ Riverside, Riverside, California.

<sup>&</sup>lt;sup>2</sup>P. Freytag, Department of Entomology, University of Kentucky, Lexington, Kentucky.

Many predatory arthropods which could be potential natural enemies of the WALH were observed in abandoned blocks but feeding by them on this pest was not documented. One immature mite was observed attacking leafhopper nymphs and was subsequently identified by E. W. Baker<sup>1</sup> as <u>Anystis</u> <u>sp</u>.

Observation indicated that the WALH was the predominant leafhopper species present throughout each growing season in commercial orchards where pesticides were applied, but the interaction of natural enemies and WALH is difficult to document in these orchards. In abandoned orchards the WALH and its natural enemies could be studied much better, but several other species of leafhoppers were present. Therefore, nymphs were collected from apple trees in abandoned orchards and reared in cages similar to those used for nymphaladult parasitoid development. These specimens were reared to adults and identified by J. P. Kramer<sup>2</sup> as <u>Typhlocyba pomaria</u> McAtee, <u>Empoasca fabae</u> (Harris), <u>Empoasca maligna</u> Walsh, and <u>Erythroneura</u> <u>lawsoniana</u> Baker. (See Appendix A for a discussion of the relative abundance and seasonal development of these species.)

In addition to these data, it was possible to study the phenology and development of the first generation nymphs of the WALH on six Red Delicious apple trees in orchard 1, in 1974. In this study.

<sup>&</sup>lt;sup>1</sup>E. W. Baker, Insect Identification and Beneficial Introduction Institute, Agricultural Research Center, West Administration Building, Beltsville, Maryland 20705.

<sup>&</sup>lt;sup>2</sup>J. P. Kramer, Insect Identification and Beneficial Introduction Institute, Agricultural Research Center, West Administration Building, Beltsville, Maryland 20705.

12 leaf clusters were marked in all directions and levels on each tree. Nymphs and last instar exuvia of the WALH were counted on the same marked leaf clusters from start to end of nymph activity in that generation. Results of these counts are presented in Table 5.

#### Material and Methods

## Sampling of Overwintering WALH Eggs

In 1976 (orchards 1-3) and in 1977 (orchard 3), branches were sampled to estimate development, hatch, and mortality of overwintering WALH eggs and the egg parasitoid An.epos. Samples were taken from late April to September. Season-long sampling was necessary to document the emergence of An. epos that occurred over several discrete time periods. These trends were preliminarily observed in 1975 and had previously been reported by McKenzie and Beirne (1972) in British Columbia for An. epos and by Steiner (1938) in New York for the closely related mymarid An. armatus, which also attack T. pomaria. In this study, a sample unit was the 75 cm apical part of a branch (see distribution studies of the overwintering population on these branches in Section IV). Sample size was 10 branches in orchards 1 and 3, and initially 10 branches in orchard 2. Later on, sample size was doubled in orchard 2 because of low WALH populations. In 1977, only orchard 3 was sampled in early season and 20 branches were sampled weekly. Samples were taken from randomly selected trees from a randomly selected branch of any height and direction, and then the sampled branch was measured to see if it met the criterion of being 75 cm or more long before it was accepted. On each branch several

variables were recorded: (1) Total T. pomaria eggs which are laid in collenchyma tissue parallel to the surface (characterised by extrusion of plant tissue) (Armstrong, 1936; Trammel, 1974). This generation of eggs of the WALH in branches can be identified from previous WALH generation eggs by the hardened extrusion of plant tissue. Also, they are distinguished from E. maligna eggs by their appearance and location on the branch. (2) Appearance of red eyes on developing egg embryos. (3) Hollow egg cavities of emerged nymphs. (4) Atrophied eggs that were degenerated. (5) Parasitoid larva distinguishable by the presence of a fat-like organel in the parasitoid body. (6) Parasitoid pupa, including well-developed adults that have not yet emerged. (7) The characteristic round emergence hole of the egg parasitoid. These characteristics of parasitoid and parasitised eggs were carefully verified in preliminary studies. They also have been well described by Mulla (1956) and Cate (1974) for An. epos and by Armstrong (1935) for An. armatus.

Percentage WALH eggs developed to the red eye stage, hatched, degenerated, and parasitised were calculated from using the following equations:

the ggs developed red eye =  $\frac{(\text{Re} + \text{N})100}{\text{TP} - (\text{D} + \text{P})}$ 

% eggs hatched =  $\frac{(N)(100)}{TP - (D + P)}$ 

% eggs degenerated =  $\frac{(D)(100)}{TP}$ 

% eggs parasitised =  $\frac{(P)(100)}{TP - D}$ 

where Re = number of eggs observed in red eye phase, N = number of eggs hatched or passed through red eye phase, TP = total eggs counted, D = eggs degenerated, P = total eggs parasitised.

# Sampling of WALH Adults

Sticky board traps (8<sup>+</sup> x 11") made from galvanized tin colored with Yellow Krylon #1801 and covered with Stickem Special @ 2 for adhesive effect were used to estimate the seasonal activity and distribution of WALH adults. These traps provided a relative estimate of WALH activity and previously were proven to be effective for seasonal distribution study of other leafhoppers (Rice & Jones, 1972; McKenzie & Beirne, 1972; Taboada et al., 1975). The number of traps used in this study was 12 in orchard 1 in 1975 and 12.6.6, respectively, in orchards 1, 2, and 3 in 1976. Traps were placed in the middle of the trees (outside to inside) and midway between the upper and lower portion, throughout the season. In 1975, traps were removed and cleaned only at the end of each generation. In 1976, traps were replaced weekly. In each case, leafhoppers were removed, washed in xylene to remove adhesive material, and stored in 75% ethanol for subsequent identification. Leafhopper species collected from each trap were identified by external morphological characters given by Ackerman and Isely (1931) and by female sternite and male genetalia

<sup>1</sup>Yellow Krylon #1801, a product by Borden, Inc., Department CP, Columbus, Ohio 43215.

<sup>2</sup>Stickem Special<sup>®</sup>, a product produced by Mapco Products, by Michel and Pelton Co., Manufacturing Chemists, Emeryville, California. as suggested by Beirne (1956) and Beamer (1930). When catch per trap for each species was more than 20, species composition was subsampled; if any problems in identification were encountered, all specimens were rechecked. Parasitism by the nymphal-adult parasitoid, <u>Ap. typhlocyba</u>, was identified by the presence of larval cyst on the WALH abdomen. Sampling of all species was begun in spring before adult WALH emergence and was ended in October when their populations were limited by cold temperatures.

#### Sampling of Summer WALH Eggs

Previous investigators (Ackerman & Isely, 1931; Armstrong, 1936) found it difficult or impossible to observe WALH summer eags. In this study, observation of summer eggs was necessary to determine the seasonal distribution, spatial distribution (Section IV), and development of WALH, to understand the impact of egg parasitism on this stage and to predict nymph emergence. To accomplish this, leaves were bleached in 75% ethanol for 24 hours, washed clean, and submerged in a petridish of water. After this treatment, WALH eggs could easily be counted under a binocular microscope in the petiol, main midrib, and large veins on the undersurface of the leaves. This method was also efficient even when egg densities were low. Its usefulness was validated in the field by its close correlation to the seasonal summer distribution of adults. Egg development and parasitised eggs were also surveyed with this ethanol treatment technique. In 1975, 14 Ida Red apple trees and in 1976 6 mix varieties of apple were randomly selected in orchard 1. On each tree 80 leaves were

sampled from upper parts, lower parts, and four cardinal directions of trees by picking 10 leaves in each of 8 quadrants. Sampling started when activity of adults was observed and continued to mid-August. Samples were taken in weekly intervals. The ethanol method proved (see Result and Discussion) to be efficient in determining more developed stages of summer eggs, but inefficient in detecting newly oviposited WALH eggs and the total number of WALH eggs at certain periods.

respect During this study, it was observed that fresh leaves kept in 40° F for 2 weeks could more readily be dissected than could fresh leaves. Also, observations by the cold temperature method showed many WALH eggs laid on the surface of the leaves in the midrib. This has not been reported by previous investigators. This possible storage effect could be improved by keeping leaves in the freezer at -5° C for 1 hour. Leaves treated in this way when beginning to thaw could easily be dissected and eggs detected. The efficiency of the ethanol technique and the improved freezing technique was compared on leaf samples taken from an orchard with a relatively high population of WALH. Three leaf samples were taken during a 1-month period. At each sampling date, 50 randomly selected leaves were checked over time. Also, known oviposition sites were compared for four location zones, petiol, midrib undersurface of the leaves, midrib on the surface of the leaf, and large veins on or under the surface of the leaves. These data were taken from the same samples to determine the relative efficiency of each technique through time.

# Result and Discussion

## Overwintering Eggs

In Tables 1, 2, 3, and 4 and Figure 1.A and B, data on the seasonal development and hatch of overwintering WALH eggs are presented. In 1976, the first eggs were observed with red eyes on April 23, 23, and 30, respectively, for orchards 1, 2, and 3, and in 1977 they were observed on April 29 in orchard 3. These counts represented 5.7, 25, 1.1, and 8.4% of the total WALH population. respectively. Overwintering egg development was very rapid. More than 90% of the population developed to this stage during 3 weeks in 1976 in orchards 1 and 3 and 2 weeks in 1977 in orchard 3. In 1976, a longer developmental period on a calendar scale in comparison to 1977 was related to a sudden cold temperature which occurred during the WALH developmental period. Its effect can be observed in Figure 1.A in the lower part of the curve for orchard 1, and in the middle of the curve in orchard 2. Overall, during favorable environmental conditions, more than 90% of the WALH egg population developed to red eye phase in 2-3 weeks. These data are consistent with those of Armstrong (1936), who noted that more than 90% of WALH nymphs emerged in a 2-week period in Ontario. This rapid development and the absence of red eyes on the embryo in early season suggested that WALH eggs do not develop appreciably in the previous fall, but remain in diapause in an early developmental state.

Another criterion for comparing overwintering egg development between orchards is the use of 50% development point. This can be interpolated from Figure 1.A. In 1976, 50% egg development was observed

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Date	Number of Samples	Total Eggs Counted	Mean ± Standard Error	% Eggs Degenerated	% Non- degenerated Eggs Parasitised	% Viable Eggs in or Past Red Eye Stage	% Viable Eggs Hatched
4/23	10	36	3.6 ± 1.37	0	2.7	5.7	0
4/30	10	21	2.1 ± 0.91	4.7	5.0	5.2	0
5/7	10	32	3.2 ± 0.79	3.2	3.2	43.3	13.3
5/14	10	45	4.5 ± 0.83	0	24.4	79.4	14.7
5/21	10	55	5.5 ± 1.51	12.7	14.5	90.2	26.8
5/28	10	61	6.1 ± 1.66	11.4	42.5	100.0	83.8
6/4	10	20	2.0 ± 0.73	30.0	21.4	100.0	100.0

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Date	Number of Samples	Total Eggs Counted	Mean ± Standard Error	% Eggs Degenerated	% Non- degenerated Eggs Parasitised	% Viable Eggs in or Past Red Eye Stage	% Viable Eggs Hatched
4/23	d	18	13.5 + 4.12	9	1_48	9	4
4/30	10	œ	0.08 ± 0.79	0	0	37.5	0
5/7	10	10	1.0 ± 0.37	0	60.09	50.0	50.0
5/14	20	56	2.8 ± 0.87	0	42.8	93.75	53.1
5/21	20	22	1.1 ± 0.32	0	36.3	100.0	78.5
5/28	20	17	0.85 ± 0.21	0	41.1	100.0	100.0

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4/23       10       135       13.5 $\pm 4.12$ 0       1.48       0       0         5/7       10       122       12.2 $\pm 2.13$ 16.3       13.7       1.1       0         5/7       10       56       5.6 $\pm 2.14$ 0       17.3       10.8       6.5         5/14       10       69       6.9 $\pm 3.23$ 0       10.1       82.2       17.7         5/14       10       176       17.6 $\pm 5.99$ 7.3       9.2       96.6       38.2         5/21       10       176       17.6 $\pm 5.99$ 7.3       9.2       96.6       38.2         5/28       10       81       8.1 $\pm 1.86$ 27.1       45.7       100.0       65.6         6/4       10       97       9.7 $\pm 2.41$ 39.1       50.8       100.0       100.0	Date	Number of Samples	Total Eggs Counted	Mean ± Standard Error	% Eggs Degenerated	% Non- degenerated Eggs	% Viable Eggs in or Past Red Eye Stage	% Viable Eggs Hatched
4/30         10         122         12.2 $\pm 2.13$ 16.3         13.7         1.1         0           5/7         10         56         5.6 $\pm 2.14$ 0         17.3         10.8         6.5           5/14         10         69         6.9 $\pm 3.23$ 0         10.1         82.2         17.7           5/14         10         69         6.9 $\pm 3.23$ 0         10.1         82.2         17.7           5/14         10         176         17.6 $\pm 5.99$ 7.3         9.2         96.6         38.2           5/28         10         81 $8.1 \pm 1.86$ 27.1         45.7         100.0         65.6           5/28         10         87         39.1         50.8         100.0         65.6	4/23	10	135	13.5 ± 4.12	% cggs Degenerated	1.48	Red Eye Stage	-
$5/7$ 10         56         5.6 ± 2.14         0         17.3         10.8         6.5 $5/14$ 10         69 $6.9 \pm 3.23$ 0         10.1         82.2         17.7 $5/21$ 10         176 $17.6 \pm 3.23$ 0         10.1         82.2         17.7 $5/21$ 10         176 $17.6 \pm 3.23$ 0         10.1         82.2         38.2 $5/21$ 10         176 $17.6 \pm 5.99$ 7.3         9.2         96.6         38.2 $5/28$ 10         81 $8.1 \pm 1.86$ $27.1$ $45.7$ 100.0         65.6 $6/4$ 10         97 $9.7 \pm 2.41$ 39.1         50.8         100.0         100.0	4/30	10	122	12.2 ± 2.13	16.3	13.7	1.1	0
$5/14$ 10     69 $6.9 \pm 3.23$ 0     10.1     82.2     17.7 $5/21$ 10     176     17.6 \pm 5.99     7.3     9.2     96.6     38.2 $5/28$ 10     81 $8.1 \pm 1.86$ 27.1 $45.7$ 100.0 $65.6$ $6/4$ 10     97 $9.7 \pm 2.41$ 39.1 $50.8$ 100.0     100.0	5/7	10	56	5.6 ± 2.14	0	17.3	10.8	6.5
5/21         10         176         17.6 $\pm$ 5.99         7.3         9.2         96.6         38.2         5/28         10         81 $\pm$ 1.86         27.1         45.7         100.0         65.6         66.6         65.6         66.6	5/14	10	69	6.9 ± 3.23	0	10.1	82.2	17.7
5/28         10         81         8.1 ± 1.86         27.1         45.7         100.0         65.6           6/4         10         97         9.7 ± 2.41         39.1         50.8         100.0         100.0	5/21	10	176	17.6 ± 5.99	7.3	9.2	96.6	38.2
6/4         10         97         9.7 ± 2.41         39.1         50.8         100.0         100.0	5/28	10	81	8.1 ± 1.86	27.1	45.7	100.0	65.6
	6/4	10	67	9.7 ± 2.41	39.1	50.8	100.0	100.0

a	Number of Samples	Total Eggs Counted	Mean ± Standard Error	% Eggs Degenerated	% Non- degenerated Eggs Parasitised	% Viable Eggs in or Past Red Eye Stage	% Viable Eggs Hatched
6	20	308	15.4 ± 3.87	20.1	8.1	8.4	0
	20	408	20.4 ± 4.84	18.3	28.2	68.6	1.6
3	20	328	16.4 ± 2.92	28.6	26.0	92.4	19.6
0	20	274	13.7 ± 2.29	25.1	27.8	99.3	93.9





May 7, 9, 11, respectively, in orchards 1, 2, and 3 and in 1977 it occurred on May 4 in orchard 3. This suggests there was more variation on a calendar date between years for the same orchards than between different orchards in the same year.

The earliest egg hatch from overwintering eggs was observed on May 7 for orchards 1 and 3 in 1976 and on May 6 in orchard 3 in 1977. Although the dates of first hatch in those orchards coincided closely. percentage hatch differed appreciably and again 50% hatch provides a better criterion for phenological comparison between orchards (Figure 1.B). Overall, there was a good correlation between the appearance of red eyes in the embryos and nymphal emergence. By sampling of the red eve stage, it appears that hatch can be anticipated. Observed variation between these two events in Figure 1.A and B can be accounted for by variation in physical environmental factors. In Section III these phenological events are averaged on a physiological time scale (degree day) to remove part of this variation. Effect of parasitism by egg parasitoid and degeneration of eggs by unknown factors are other factors influencing these variations. Information on parasitism relative to pest phenology was relatively limited, but their influence will be discussed later.

The effect of degeneration of eggs can be closely linked to physical environmental factors. Causes for degeneration of WALH eggs are not known, but they have been related to factors such as growth of plant tissue, differential effect of low temperature on different phases of egg development, the incidence of nonfertilized eggs, and

egg predation. Variable plant growth features are most suspect because the highest levels of degeneration were observed in orchard 3, which was given a standard horticultural treatment. Also, environmental temperature could directly or indirectly have increased the number of eggs degenerated. Nonfertilization of eggs cannot be the main factor, because in this study eggs with well-developed embryos were also degenerated. Egg predators are least suspect because the highest levels of egg degeneration were observed in orchard 3. This orchard was treated with sprays and had a small insect fauna. Parasitisation of eggs by the egg parasitoid when eggs are partially developed (see later discussion) as an explanation could be added to this list. This phenomenon has been associated with the same parasitoid on grape leafhopper (McKenzie & Beirne, 1972). The percentage of eggs degenerated during the study period is presented in Tables 1, 2, 3, 4, and 22.

## Nymph Activity

In this study, sampling of nymphal populations did not receive primary emphasis; however, limited observations of nymphal activity were taken. In 1974, the first nymph was observed on May 27, and at this time 34.8% of all nymphs were emerged (Table 5), and 50% nymph emergence was estimated to occur on May 29. The first of the fifth instar exuvia (representing start of adult activity) was observed on June 14 (Table 5) and 50% exuvia accumulation was estimated on June 23. These data suggest that there are 26 days between first nymph emergence to appearance of adults. The delay in nymph emergence in this orchard (orchard 1, 1974) was correlated with unfavorable temperature early in

Date	Small <sup>a</sup> Nymphs	Large <sup>b</sup> Nymphs	Exuvia	Total Nymphs + Exuvia	% Accu- mulation Emergence	% Accu- mulation Exuvia
5/20	0	0	0	0	0	0
5/27	15	0	0	15	34.8	0
6/3	42	0	0	42	97.6	0
6/14	24	15	4	43 <sup>d</sup>	100.0	10.2
6/19	4 <sup>C</sup>	30	5	39		12.8
6/26	0	12	28	38		71.7
7/3	0	3	38	41		97.4
7/10	0	0	39	39 <sup>d</sup>		100.0

Table 5.--Emergence and development of first generation nymphs of the  $\underline{T}$ . pomaria in orchard  $\underline{1}$ , 1974.

<sup>a</sup>Wing pads not developed.

<sup>b</sup>Wing pads developed.

<sup>C</sup>Small nymphs were suspect for <u>E</u>. <u>fabae</u>.

 $^{\rm d}{\rm Number}$  of exuvia were only four (9.3%) less than number of nymphs.

the season in that year. In this study (previous discussion, preliminary studies), the maximum number of nymphs counted and maximum number of last instar exuvia counted indicated that mortality of nymphs through nymphal maturation was low. Also, if any immigration-emigration took place after nymphs became established on the leaves, it was approximately equal. Also, these data suggested that last instar exuvia were persistent on the leaves, and in the end of the nymph activity period, only 9.3% of exuvia were lost. The nonmigratory habits of the nymphs and persistence of the last instar exuvia on the same leaves, as suggested by Armstrong (1936), were verified in this experiment. Second generation nymph emergence was observed during the last 2 weeks of July. It peaked in the first 2 weeks of August in different localities. More precise estimates of this activity were obtained from egg developmental data (Section III).

# Activity of WALH Adults

Adult population data for both generations are given in Tables 6-13 and plotted in Figures 2-9. In orchard 1--1975 (Tables 6, 7, and Figures 2 and 3), adult activity started in the second week of June and increased very rapidly. Rapid build-up of adults was possibly because of synchronized maturation of nymphs which emerged over a 2-3 week period. Results in orchard 1--1976 (Tables 8, 9, Figures 4 and 5) were similar and only small differences were observed in the magnitude of trap catch and the dates when activity started. In orchard 2--1976 (Tables 10, 11, Figures 6 and 7), the start of activity was recorded the same day as in orchard 1 in 1976, but mean capture per trap in orchard 2

Date	Sample Size	Mean ± Standard Error	Variance	Total Parasitised
6/13	12	0.17 ± 0.11	0.15	0
6/21	12	3.83 ± 0.69	5.79	0
6/28	12	4.33 ± 1.12	15.15	1
7/5	12	5.67 ± 1.20	17.15	2
7/12	12	3.83 ± 0.73	6.33	0
7/19	12	$2.08 \pm 0.48$	2.81	1
7/26	12	2.17 ± 0.34	1.42	0
8/2	12	0.83 ± 0.27	0.88	0
8/9	12	$0.75 \pm 0.23$	0.68	0
8/16	12	1.00 ± 0.33	1.27	0
8/23	12	0.50 ± 0.19	0.45	0
8/30	12	1.33 ± <sup>a</sup>	a	0
9/7	12	$5.50 \pm 0.80$	7.73	2
9/14	12	7.42 ± 1.15	15.90	2
9/21	12	16.00 ± 1.94	45.27	8
9/28	12	22.08 ± 4.36	228.08	6
10/5	12	18.17 ± 3.32	132.33	6
10/12	12	18.17 ± 2.93	103.24	3
10/19	12	12.83 ± 2.54	77.61	١

Table 6.--Mean number adult <u>T</u>. <u>pomaria</u> and total parasitised adult <u>T</u>. <u>pomaria</u> captured on yellow traps in orchard 1, 1975.

<sup>a</sup>Variation was not calculated.



	atch	o4dp o4+dc	0.69	16.66	34.72	58.33	74.30	82.98	92.01	95.48	98.26 0.08	100.00 0.64	1.13	2.43	3 7.79	5 15.01	30.60	5 52.11	4 69.80	3 87.50	100.00
	% Accumulation C	,よ <sup>4</sup> な	0.00	1.67	16.20	40.22	61.45	73.74	87.15	92.73	97.20	100.00		0.5	2.8	5.6	17.4	30.6	47.6	76.8	0.001
cnaru I, 19/0.		O <sup>ab</sup> တို	1.83	41.28	65.13	88.07	95.41	98.16	100.00	:	0.1	0.78	1.37	2.84	8.82	16.96	33.33	56.56	74.41	89.70	100.001
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		uate	6/13	6/21	6/28	7/5	7/12	61/1	7/26	8/2	8/9	8/16	8/23	8/30	9/7	9/14	9/21	9/28	10/5	10/12	01/01

Table 7.--Total weekly catch and % accumulation of T. pomaria adults for each generation,

<sup>a</sup>End of activity for first generation. <sup>b</sup>First generation.

<sup>C</sup>Second generation.

d<sub>Estimated</sub>.





Date	Sample Size	Mean ± Standard Error	Variance	Total Parasitised
6/11	12	0.58 ± <sup>a</sup>	<sup>a</sup>	0
6/18	12	10.92 ± 1.83	40.27	0
6/25	12	43.75 ± 6.83	558.75	2
7/3	12	20.25 ± 3.28	129.30	7
7/10	12	20.42 ± 3.66	160.45	3
7/17	12	7.83 ± 1.66	32.88	0
7/24	12	7.00 ± 1.54	28.55	0
8/3	12	4.25 ± 0.64	4.93	0
8/10	12	2.42 ± 0.66	5.17	0
8/18	12	0.25 ± 0.18	0.39	0
8/25	12	0.67 ± 0.22	0.61	0
9/1	12	$3.08 \pm 0.68$	5.54	0
9/9	12	20.25 ± 2.24	60.20	2
9/16	12	27.33 ± 3.70	164.06	12
9/23	12	32.83 ± 5.64	381.61	15
9/30	12	9.67 ± 2.10	52.97	4
10/7	12	28.92 ± 3.00	107.90	1
10/14	12	7.92 ± 1.57	29.54	0
10/21	12	0.66 ± <sup>a</sup>	<sup>a</sup>	0

Table 8.--Mean number adult <u>T</u>. <u>pomaria</u> and total parasitised adult <u>T</u>. <u>pomaria</u> captured on yellow traps in orchard 1, 1976.

<sup>a</sup>Variation was not calculated.





<b>O</b> <sup><b>a</b></sup> b <b>O</b> <sup><b>a</b></sup> c <b>1.03</b> <b>18.61</b> <b>18.61</b> <b>18.61</b> <b>18.61</b> <b>90.1</b> <b>91.93</b> <b>92.26</b> <b>93.75</b> <b>93.75</b> <b>93.75</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>93.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>103.7</b> <b>1</b>	Catth 12 100 200 200 200 200	Atch     O       0     1.03       12     18.61       12     18.61       12     18.61       12     18.61       12     18.61       12     18.61       12     18.61       12     18.61       12     18.61       12     18.61       12     18.61       13     100.00       27     100.00	0 <sup>9</sup> 8 - 8 9 9	<b>P</b> b <b>P</b>	c O <sup>3+</sup> Q <sup>b</sup> 9.70 9.70 64.10 64.10 81.50 88.10 94.10
1.03 18.61 81.38 90.1 96.75 97.93 99.7 99.7 99.7 100.00 <sup>a</sup> 4.13 4.13 50.36	0 12 100 200 86	0 1.03 12 18.61 184 90.1 200 96.75 26.75 275 99.26 27 99.26 27 100.00	o 0 0 0 0 0 - 0	0.00 1.60 40.2 67.40 89.30 95.9	0.49 9.70 46.90 64.10 81.50 88.10 94.10
18.61 81.38 90.1 96.75 97.93 99.7 99.7 99.7 100.00 <sup>a</sup> 4.13 4.13 50.36	12 100 200 86	12         18.61           100         81.38           184         90.1           186         96.75           200         96.75           215         99.26           27         190.00	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	1.60 15.20 40.2 79.10 89.30 89.30	9.70 46.90 64.10 81.50 88.10 94.10
81.38 90.1 96.75 97.93 99.7 99.7 100.00 <sup>a</sup> 4.13 4.13 50.36	100 184 86	100         81.38           184         90.1           200         96.75           200         96.75           200         96.75           200         96.75           200         96.75           21         99.26           27         99.26           27         99.26           27         100.00	0 0 0 9 0 0	15.20 40.2 67.40 89.30 95.9	46.90 64.10 81.50 88.10 94.10
90.1 96.75 97.93 99.26 99.7 99.7 100.00 <sup>a</sup> 4.13 4.13 50.36	184 200 86	184         90.1           200         96.75           86         97.93           75         99.26           48         99.7           27         100.00	م م م م	40.2 67.40 79.10 89.30 95.9	64.10 81.50 88.10 94.10
96.75 97.93 99.26 99.7 99.7 100.00 <sup>a</sup> 4.13 4.13 50.36	200 86	200 96.75 86 97.93 75 99.26 48 99.7 27 100.00	റ്റ്റ്റ്റ്റ്റ്റ്റ്റ്റ്റ്റ്റ്റ്റ്റ്റ്റ്	67.40 79.10 89.30 95.9	81.50 88.10 94.10
97.93 99.26 99.7 100.00 <sup>a</sup> 4.13 4.13 50.36	86	86 97.93 75 99.26 48 99.7 27 100.00	o <sup>a</sup> e a	79.10 89.30 95.9 00 50	88.10 94.10
99.26 99.7 100.00 <sup>a</sup> 4.13 4.13 24.54 50.36		75 99.26 48 99.7 27 100.00	б О <sup>а</sup>	89.30 95.9 00.50	94.10
99.7 100.00 <sup>a</sup> 0.73 4.13 24.54 50.36	75	48 99.7 27 100.00	Da	95.9 00 FN	
a 100.00 <sup>4</sup> 0.73 4.13 24.54 50.36	48	27 100.00	04	00 50	97.70
a 0.73 4.13 24.54 50.36	27			<b>00.</b> 00	99.70
0.73 4.13 24.54 50.36	3a 3	3a		100.00 <sup>a</sup>	100.00 <sup>a</sup>
4.13 24.54 50.36	0	0	0.73		
24.54 50.36	0	0	4.13		
50.36	21	21	24.54	4	.30
	47	47	50.36	13.	6
78.49	88	88	78.49	31.	.90
83.91	57	57	83.91	43.	.60
98.16	192	92	98.16	82.	.90
100.00	75	75	100.00	98.	.30
100.00	∞	8	100.00	100.	00

Table 9.--Total weekly catch and % accumulation of T. pomaria adults for each generation, captured

<sup>a</sup>End of activity for first generation. <sup>b</sup>First generation.

<sup>C</sup>Second generation.



Figure 5.--Cumulative percentage trap catch <u>T</u>. <u>pomaria</u> for males and females together and separately in orchard 1, 1976.

Date	Sample Size	Mean ± Standard Error	Variance	Total Parasitised
6/11	6	1.00 ± <sup>a</sup>	a	0
6/18	6	4.67 ± 1.02	6.27	0
6/25	6	17.17 ± 3.24	62.97	2
7/2	6	10.83 ± 2.44	35.77	1
7/10	6	13.50 ± 1.20	8.70	0
7/17	6	4.17 ± 1.45	12.57	0
7/24	6	3.50 ± 1.52	13.90	0
8/3	6	2.67 ± 0.80	3.87	0
8/11	6	1.33 ± 0.56	1.87	0
8/18	6	0.17 ± 0.17	0.17	0
8/25	6	0.33 ± 0.33	0.67	0
9/1	6	0.33 ± 0.21	0.27	0
9/9	6	7.00 ± 2.27	30.80	1
9/16	6	8.17 ± 1.74	18.17	3
9/23	6	8.33 ± 2.09	26.27	3
9/30	6	11.17 ± 2.21	29.37	3
10/7	6	7.00 ± 1.69	17.20	3
10/14	6	5.00 ± 1.15	8.00	0
10/21	6	1.66 ± <sup>a</sup>	<sup>a</sup>	0

Table	10Mean n	umber adu	lt T. pomar	ia and tota	al parasitised	l adult
	<u>T. pom</u>	<u>naria</u> captu	ured on yel	low traps	in orchard 2,	1976.

<sup>a</sup>Variation was not recorded.





		ں 4+0 د										0.30	1.00	1.60	5.90	2.50	9.40	2.20	5.40	5.60	0.00
		δ										-	-	-	~	ñ	4	2	æ	6	0
		at da ot teo	1.60	9.60	38.80	57.20	80.10	87.20	93.20	97.70	100.00										
	ation Catcl	ი ი											0.50	0.50	7.90	20.30	38.40	59.30	77.90	94.30	100.00
	% Accumula	م ¢		6.30	24.10	34.70	57.40	73.00	85.10	94.30	100.00										
		°°¢										0.84	1.69	3.38	27.96	50.84	66.10	91.52	99.15	100.00	
, 1976.		o <sup>a</sup> p	2.83	11.79	48.58	72.16	95.28	96.69	98.58	100.00											
orchard 2,	С	catch	0	6	25	15	32	22	17	13	8 <b>9</b>	0	-	0	13	22	32	37	33	29	10
traps in	\$	Catch	9	61	78	50	49	ო	4	3a	0	-	~	2	29	27	18	30	6	~	0
on yellow	0 + <b>5</b>	Catch	9	28	103	65	81	25	21	16	∞	-	2	2	42	49	50	67	42	30	10
		Date	11/9	6/18	6/25	7/2	01/2	<b>71/7</b>	7/24	8/3	8/11	8/18	8/25	6/۱	6/6	9/16	9/23	9/30	10/7	10/14	10/21

Table 11.--Total weekly catch and % accumulation of I. pomaria adults for each generation, captured

<sup>a</sup>End of activity for first generation. <sup>b</sup>First generation.

<sup>c</sup>Second generation.





Date	Sample Size	Mean ± Standard Error	Variance	Total Parasitised
6/11	6	0.00 ± 0.00	0	0
6/18	6	5.33 ± 0.21	0.27	0
6/25	6	14.50 ± 5.42	176.30	0
7/3	6	6.83 ± 2.82	47.77	0
7/10	6	2.33 ± 0.88	4.67	0
7/17	6	0.67 ± 0.49	1.47	0
7/24	6	0.17 ± 0.17	0.17	0
8/3	6	0.00 ± 0.00	0	0
8/10	6	0.17 ± 0.17	0.17	0
8/18	6	0.17 ± 0.17	0.17	0
8/25	6	0.00 ± 0.00	0	0
9/1	6	9.50 ± 4.76	135.90	0
9/9	6	35.50 ± 12.10	879.10	0
9/16	6	32.50 ± 9.42	532.30	0
9/23	6	34.50 ± 8.85	469.90	0
9/30	6	52.67 ± 8.76	460.27	0
10/7	6	55.67 ± 11.18	750.27	1
10/14	6	43.17 ± 7.85	370.17	1
10/21	6	8.16 ± <sup>a</sup>	a	0

Table 12.--Mean number adult <u>T</u>. <u>pomaria</u> and total parasitised adult <u>T</u>. <u>pomaria</u> captured on yellow traps in orchard 3, 1976.

<sup>a</sup>Variation was not calculated.



	on yellow	traps in	orchard 3,	1976.					
	0+00	δ	0			% Accumul	ation Catc	£	
Date	Catch	Catch	Catch	δ <sup>₽</sup>	о <sup>°</sup> с	ء <del>م</del>	ა 어	° ↓ v	°, to
6/11	0	0	0	00.0		0.00		0.00	
6/18	32	32	0	22.22		0.00		17.60	
6/25	87	84	m	80.55		8.10		65.70	
7/3	41	22	19	95.83		59.40		88.30	
7/10	14	4	10	98.61		86.40		96.10	
71/7	4	2ª	2	100.00		91.80		98.30	
7/24	-	0	-			94.50		98.80	
8/3	0	0	0			94.50		98.80	
8/10	-	0	-			97.20		99.40	
8/18	-	0	ןם			100.00		100.001	
8/25	0	0	0						
1/6	57	52	5		6.67		0.50		3.40
6/6	213	771	36		29.39		4.80		16.50
9/16	195	119	76		44.67		13.70		28.50
9/23	207	122	85		60.33		23.70		41.20
9/30	316	138	178		78.04		44.60		60.60
10/7	334	81	253		88.44		74.30		81.10
10/14	259	79	180		98.58		95.50		96.90
10/21	49	=	38		100.00		100.00		100.00

Table 13.--Total weekly catch and % accumulation of T. pomaria adults for each generation, captured

<sup>a</sup>End of activity for first generation. <sup>b</sup>First generation.

<sup>c</sup>Second generation.





was higher than orchard 1 at the same date. Total catch per generation was higher in orchard 1. These data suggested that adult emergence had already begun earlier in orchard 2. This was expected because orchard 2 is more southernly located and egg hatch in this orchard was earlier in comparison to orchard 1. In orchard 3--1976 (Tables 12, 13, Figures 8 and 9), the initial pattern of adult activity was changed somewhat, probably because of pesticide application. Peak activity, however, in this orchard was the same as in the other orchards.

In orchard 1--1975, males started and ended their activity sooner than females (Figure 3), and males were active for 7 weeks while females were active for 9 weeks. This suggests a longer longevity for females than males. This pattern of behavior in orchards 1, 2, and 3 in 1976 was similar to that observed in orchard 1 in 1975, but the duration of activity was slightly different in each case. These results are consistent with data reported from rearing studies by Armstrong (1936) and Ackerman and Isely (1931). They noted that male activity started sooner and that females had a longer longevity. Estimates of sex ratio can be obtained by comparing peak activity of the two sexes for each They often favored males in the first generation. This orchard. may be related to the inherent characteristic of species in response to environmental factors for activity or differences in response of each sex to the yellow-colored traps. The problems of data interpretation are discussed by Southwood (1966) when different sex

ratios are recorded for insects when yellow traps and other relative density estimation techniques are used. Activity of females in first generation may continue to August, but more than 90% activity ended in late July (Figures 3, 5, 7, 9). Since a 6-day postoviposition period is reported for females (Armstrong, 1936), we can expect oviposition of the female population to end in late July.

In orchard 1--1975, second generation adult activity started in the second week of August, peaked at the end of September, and ended on October 19 when the population was limited by cold tempera-In orchard 1--1976, activity of second generation adult WALH ture. lagged in comparison to 1975. This was correlated with a delay in summer egg development in 1976 in comparison to 1975 (Tables 14 and In orchard 2--1976, activity started sooner than in orchards 15). 1 and 3. The more gradual build up of the adult population in this generation was expected due to increased population variance and low temperature in late season. The rapid rise in population activity in orchard 3 was partly an artifact of a modified sampling plan. During the second generation, adult activity was observed in a hot spot in the western part of the orchard, but trap catches were not recorded. Traps were thereafter removed and redistributed in the western part of the block. These data were biased in comparison to other orchards, but at least they provided information on late season activity in orchard 3. In all orchards except orchard 3, male activity was initiated earlier than female activity. Only in orchard 2 did both sexes complete the generation before cool
Table 14	<pre>tSeasonal distribution orchard l, 1975.a</pre>	of first generation egg	s of <u>T</u> . <u>pomaria</u> in
Date	Number of Leaves Sampled	Total Eggs Counted	Total Eggs Developed Red Eyes
7/6	1,120	-	0
7/13	1,120	æ	0
7/20	1,120	13 <sup>b</sup>	-
7/27	1,120	22 <sup>b</sup>	4
8/3	1,120	39 <sup>b</sup>	18
8/10	1,120	26	16
8/17	1,120	ω	Q
	<sup>a</sup> Host plants were Ida Re	d apple variety.	

b<sub>On</sub> each date one parasitised egg was observed.

Table l	5Seasonal d orchard 1,	listribution 1976. <sup>a</sup>	of first generation eggs	of <u>T</u> . <u>pomaria</u> in
Date	Numb Leaves	er of Sampled	Total Eggs Counted	Total Eggs Developed Red Eyes
01/7		480	2	O
71/2		480	ĸ	o
7/24		480	18	4
8/3		480	25	ω
8/10		480	34	15
8/18		480	14	נו
8/25		480	ĸ	0
	<sup>a</sup> Host plants	were mixed v	arieties of apple trees.	

temperatures terminated further flight. In orchards 1 and 3, male populations completed the entire generation; however, female populations were subjected to cold temperature and suffered high mortality in October. The sex ratio in the second generation was variable between orchards and was affected by the factors discussed relative to the first generation (see earlier discussion). Overall, the WALH has two discrete generations in Michigan. There is only a slight overlap between the late female individuals of the first generation and the early male individuals of the second generation, but these forms can readily be distinguished.

As a sampling tool, the yellow sticky board traps provided consistent data on the phenology of this species in undisturbed orchards. When 12 traps were used and the mean WALH density per trap was more than 5 individuals, standard error as percentage of the mean was less than 25 and it varied between 10-20% at higher densities (Figure 10.A and B). This was the case in orchard 1 in 1975 and 1976. When six traps were used per orchard, the degree of precision was less. An average density of 8 WALH per trap was necessary before the standard error of means fell below 25%. This was observed in orchard 2 (Figure 11.A). In orchard 3 (representative of a commercial sprayed orchard), the degree of precision was more variable (Figure 11.B). These data in Figures 10 and 11 suggest that yellow sticky board traps are useful for seasonal distribution study and the determination of the activity of the WALH as has been observed in sampling other leafhopper species (Rice & Jones, 1972;



Figure 10.--The degree of precision with which the mean  $\underline{T}$ . pomaria trap catch is defined for 12 traps.



Figure 11.--The degree of precision with which the mean  $\underline{T}$ . pomaria trap catch is defined for six traps.

McKenzie & Beirne, 1972; Taboada et al., 1975). The behavioral response of the leafhopper to this type of trap is poorly understood. If absolute density estimates by this sampling method are to be useful, the attractive effect and relative catching efficiency of these traps should be investigated over a wide range of densities and environmental conditions.

### Summer WALH Eggs

In orchard 1--1975, the first summer egg was observed on July 6 and the population peaked on August 3 (Table 14). The first female WALH adult had been captured on June 21 and the population peaked on July 5 (Table 7). The same events in orchard 1--1976 occurred, respectively, on June 10, August 10, June 18, and July 10 (Tables 9, 15). These relationships initially suggested that the seasonal distribution of recorded eggs was poorly correlated with the seasonal distribution of female WALH adults. Since the preoviposition period of WALH is 9-13.4 days (Armstrong, 1936), this may partially account for the lagged seasonal distribution of summer eggs, but not entirely because data showed a 15-31 days delay between adult female activity and oviposition. Cool temperatures, long intervals between samplings, possibility of overlap in oviposition by other species of leafhoppers, and errors in egg detection were hypothesized possibly to account for this delay in detecting the summer eggs. More detailed examination of data revealed that temperature during activity of WALH adults was sufficiently high to discount its effect on the observed delay in oviposition. Sampling frequency was on the order of 7 days; thus

this reason was also considered insufficient. Other species of leafhoppers commonly associated with the WALH in apple orchards and which lay eggs in the leaves are E. fabae and E. lawsoniana. E. fabae has the same oviposition site as does the WALH in the petiol, midrib, and large veins under the surface of the leaves, but E. lawsoniana lays its eggs under the epidermis of the leaves (Ackerman & Isely, 1931). Data on the seasonal distribution of adult female T. pomaria (Tables 7 and 9), E. fabae (Tables 41 and 42), and E. lawsoniana (Tables 43 and 44) are plotted (Figures 12 and 13) versus the seasonal distribution of recorded eggs in the same orchard. The distributions of recorded eggs are less correlated with E. fabae as compared to T. pomaria, but seem to be closely correlated with E. lawsoniana. As previously described, the oviposition site of the last two species differs. However, biological research on the two species is incomplete; thus there is still some question as to whether the observed differences can be attributed to this factor.

Inefficient sampling was believed to be the main source of error contributing to the variation observed in the seasonal distribution of eggs. To test this hypothesis, freezing, thawing, and dissection of leaves provided an alternative technique for estimating eggs in leaf tissues. Efficiency comparisons of the freezing method with the ethanol bleaching method through time are presented in Table 16. Data relative to the distribution of eggs in the leaves are given in Table 17. These data suggest that not all eggs are visible early in the season, if the bleaching technique is used. However, these eggs



Figure 12.--Seasonal distribution of three species of leafhoppers, eggs laid in leaf tissue, and oviposition trend of <u>T</u>. <u>pomaria</u>, orchard 1, 1975.



Figure 13.--Seasonal distribution of three species of leafhoppers, eggs laid in leaf tissue, and oviposition trend of  $\underline{T}$ . pomaria, orchard 1, 1976.

Table 16Com thr	parison of two egg ough time.	detecting techniques	for summer eggs (	of <u>T</u> . <u>pomaria</u> ,
Sampling Date	Technique	Total Leaves <sup>a</sup> Per Technique Per Date	Total Eggs Counted	Number of Eggs Developed Red Eyes
2713C17	Bleaching	50	5	0
///e1//	Freezing	50	84	0
<i>LL10611</i>	Bleaching	50	31	Q
11/06/1	Freezing	50	182	15
2276170	Bleaching	50	140	85
11/01/0	Freezing	50	192	121
a,				

Leaf samples were collected in a commercial apple orchard.

of	e 4 <sup>d</sup>	2	n
ent zones pooled for	Zon		
n four differ 150 leaves,	Zone 3 <sup>C</sup>	10	159
f <u>T. pomaria</u> in to <u>t</u> al count on	Zone 2 <sup>b</sup>	37	165
n of summer eggs o . Each count is ng times.	Zone l <sup>a</sup>	127	131
Table 17Distributic apple leaves three sampli		Bleaching	Freezing

<sup>a</sup>Midrib under surface of the leaf.

<sup>b</sup>Petiol of the leaf.

<sup>C</sup>Midrib on the surface of the leaf.

<sup>d</sup>Large veins that were easy to dissect under surface or on the surface of the leaf.

62

0.65

34.72

36.03

28.60

Relative frequency of eggs found in each zone by

freezing technique

can be detected by the freezing technique. The efficiency of the ethanol bleaching technique increased as the eggs were further developed. Relative to the morphological and developmental characteristics of leafhopper eggs (Ackerman & Isely, 1931), WALH eggs are semi-transparent when they are laid. Later they become a milky color and finally the red eyes appear on the developing embryo. Dyes have been used for detecting other organisms and leafhopper eggs in plant tissue (Curtis, 1942; Carlson & Hibbs, 1963; Chatterjee & Ram, 1970). In our study, recorded eggs were restricted to those in the milky color stage or after individuals had developed to the red eye stage. Therefore, it was assumed that the observed delay in detection of WALH eggs was related to their invisibility while they were in the early transparent stage. Also, data on the distribution of eggs in four different zones of the leaves suggested that the ethanol bleaching technique was relatively inefficient in detecting eggs on the surface of the leaves in the midrib area (Table 17).

The above data indicated that only a portion of the actual summer egg population of the WALH had been surveyed, and observed population trends were a relative estimate of certain later stages of egg development rather than the actual oviposition trend. These techniques should be developed further if an absolute estimate of summer eggs is to be obtained. At present, the number of eggs developed to the red eye stage can be useful in predicting nymphal emergence in the WALH second generation. This subject is discussed further in Section III.

During this study, three other forms of insect-like eggs were found in the midribs of apple leaves. In the presence of <u>E. fabae</u> but when <u>T. pomaria</u> is absent, the characteristic eggs of <u>E. fabae</u> as described by Ackerman and Isely (1931) were found and identified. The second form of eggs observed was vase shaped. They appeared similar to eggs reported characteristically for Hemipterans. The third form of eggs observed was more leafhopper-like in form and was half the size of the WALH eggs. They were observed in the presence and absence of the WALH. Also, parasitised eggs were easily distinguished by the brown coloration of the pupa. Parasitised eggs will be discussed later in this section.

### Egg Parasitoid of the WALH

Observations in 1975 showed that <u>An</u>. <u>epos</u> overwintered as a half-grown larvae in the overwintering eggs of the WALH. Some individuals developed to the pupal stage early in the season and adult parasitoids emerged in synchronization with the overwintering egg hatch of the WALH. A second group of parasitoid larvae developed to pupae and emerged as adults in early summer. The remaining parasitoid larvae completed their development late in the summer.

Data taken to validate these periods of parasitoid development and emergence and to determine the precise timing of these activities are tabulated in Tables 18, 19, and 20. The three periods of parasitoid emergence occurred in orchard 1 (Table 18) from April 23 to May 28, June 25 to July 10, and after September 9. For orchard 2, data were taken too late to determine the start of the

ria in orchard 1, 1976.	Remark	Emergence hole on older woods Pupa on older woods Larva on older woods Adult well developed
eggs of <u>T</u> . <u>poma</u>	Emergence Holes	00-NM <u>-</u> -®N000-00000000
verwintering	Pupal Stage	-000000-00000000000000000000000000000
<u>A. epos</u> in o	Larval Stage	о-оө <sup>м</sup> -илаиимиом40- <i>ми</i> о
18Development of	Total Parasitised Eggs	∟∟్∠ <sup>బ</sup> బచెంటఌట⊗ంఒ₄ం⊢టచ్⊗
Table	Date	8/10 9/16 9/16 9/16 9/16 9/16 9/16 9/16 9/16

n orchard 2, 1976.	Remark	arasitised eggs observed arva on older woods dult well developed upa on older woods mergence hole on older woods upa on older woods	Hergence note on viver would
<u>T. pomaria</u> in	lence es		
g eggs of	Emerg Hol	000000000000000000000000000000000000000	5
verwinterin	Pupal Stage	0050-00-0000000-00-	-
<u>A. epos</u> in o	Larval Stage	о-б <u>ы-</u> ииори4-wppиио.	-
Development of <u>i</u>	Total Parasitised Eggs	0048700-700-8500 20048700-700-8500	7
Table 19	Date	4/30 5/14 5/13 5/21 5/28 6/1 7/17 8/18 8/25 8/25 8/25 9/1 9/1	9/10

ia in orchard 3, 1976.	Remarks	Emergence holes on older woods Pupa on older woods One adult making emergence holes Emergence hole on older woods	Larva on older woods
eggs of <u>T</u> . <u>pomar</u>	Emergence Holes	08708-25-00000	0000-
verwintering (	Pupal Stage	0-0000-00000	0000%4
<u>A. epos</u> in o	Larval Stage	2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2	30-152-0
Development of	Total Parasitised Eggs	14 2 30 2 3 2 2 3 7 2 2 2 3 2 2 2 2 2 2 2 2 2 2	2 5 7 2 5 5 5 5 5 5 5 5 5 5 5 5 5 5 5 5
Table 2(	Date	4/23 5/7 5/7 5/21 5/28 6/1 6/11 7/17 7/17 7/17 7/17 7/17 7/17	8/18 8/25 9/1 9/16

the first developmental period, but this period ended on May 28. The second period began June 18 and ended July 10, and the third continued after August 28. In orchard 3 (Table 20), April 30 to June 4, June 25 to July 10, and after September 9 were the three periods of adult emergence. Because of the low parasitoid population density observed in this study, estimates for first pupation as well as first emergence were probably late relative to the actual occurrence of these events. Therefore, both stages were considered to reflect the start of adult activity. Two to 3 weeks are necessary for parasitoid emergence holes to collapse and be filled in by plant tissue growth. Therefore, 1 week beyond the observation of the last observed parasitoid pupa was used as an estimate of parasitoid adult emergence. On the basis of these assumptions, Figure 14 is the pooled estimates for adult parasitoid emergence in the three experimental orchards during 1976.

The emergence of the first parasitoid group would seem to be out of synchrony relative to the WALH, unless emerged adult parasitoids were able to parasitise available overwintering WALH's eggs in the spring. Also, if possible, they may disperse to an alternative host and redisperse back to parasitise WALH's eggs later in the growing season. At present there is little information available on the interaction of these species in the apple orchards with those in other habitats. However, McKenzie and Beirne (1972) noted that eggs of the grape leafhopper in the vicinity of apple orchards were more heavily parasitised by <u>An. epos</u>. They hypothesized





that this species dispersed from apple orchards to vineyards. They did not document whether this parasitoid redispersed back to the apple orchards. Dispersal of this parasitoid from rubus leafhopper eggs on blackberry back to grape leafhopper eggs also has been extensively documented by Doutt and Nakata (1973).

For <u>An</u>. <u>epos</u>, 11 alternative leafhopper hosts have been reported (Peck, 1963). Six of these leafhoppers are reported in the leafhopper fauna of Michigan (Taboada, 1964). Therefore, generally speaking, the early emergence period of this parasitoid from apple should have great survival value for this species and allow it to attack many hosts. However, its contribution to the biological control of the WALH early in the season is questionable. The interaction of <u>An</u>. <u>epos</u> with the WALH and alternative hosts during early season needs to be investigated in more detail. During this study, <u>An</u>. <u>epos</u><sup>1</sup> was reared from grape leafhopper eggs on grape and from green apple leafhopper (<u>E</u>. <u>maligna</u>) on apple. <u>E</u>. <u>maligna</u> is an additional host for <u>An</u>. <u>epos</u> in addition to 11 leafhopper species reported by Peck (1963). In Table 21, egg parasitoids reared from eggs of different leafhopper species are reviewed.

Emergence of the second pulse of <u>An</u>. <u>epos</u> was synchronized with emergence of first generation female WALH. Considering that the emergence of this parasitoid spans a period of 4 weeks and the incubation period of summer eggs of the WALH averages 39 days,

<sup>&</sup>lt;sup>1</sup>Identified by G. Gordh, Department of Entomology, University of California/Riverside, Riverside, California.

it can be concluded that emergence of this parasitoid is closely synchronized with the development of summer eggs of the WALH. If <u>An. epos</u> is well adapted to this host in other ways, such as in host finding and in host selection, a high percentage of parasitism of summer eggs would be expected. This was not observed in this study. In weekly samples of summer eggs (Table 14), only one parasitised egg was found on July 20, 27, and August 3 of 1975. In addition, occasional emergence holes of this species were observed on the midrib of apple leaves in commercial orchards. We were unable to rear this parasitoid from summer eggs for identification.

<u></u>		<u> </u>	Parasitoid	
Host Plant	Host	A. epos	A. <u>armatus</u>	A Species of Trichogram- matidae
Apple	<u>T. pomaria</u>	+	-	-
Apple	<u>E. maligna</u>	+	+	+
Grape	Grape leafhopper	+	-	-

Table 21.--Egg parasitoids reared from three species of leafhoppers in Michigan apple orchards.

Key: + = association proved.

- = association not proved.

Emergence of the third group of parasitoids is synchronized with the emergence of female WALH in the second summer generation. Overwintering host eggs are available at this time and An.epos causes its highest mortality in this phase of interaction. The rationale to explain this high mortality on overwintering eggs in comparison to summer eggs of the WALH is the following: (1) Progeny of the parasitoid are most closely distributed spatially to the host at this stage (see Section IV). (2) Adult parasitoids may emerge from leafhopper hosts that overwinter as adults and may use WALH eggs as an alternative refuge; e.g., emergence of An.epos from grape leafhopper was observed through August and September in orchard 2--1977. The dynamics of this dispersal behavior from grape to apple should be investigated in more detail. (3) The differential surface area that parasitoids have to search for host in summer on the leaves versus in fall on wood of young branches may influence the effective parasitism of An.epos. It is expected that total surface area available for oviposition site of the WALH would be much larger during summer on leaves than in fall on the bark. This could increase the probability of host finding for parasitoid relative to overwintering eggs.

In summary, the effect of <u>An</u>. <u>epos</u> on the overwintering eggs of the WALH can be estimated only when overwintering egg hatch of the leafhoppers is completed and parasitised eggs can be identified by the presence of uncollapsed emergence holes and number of parasitoids present in host eggs. In 1974, 40.9% of eggs were parasitised

in orchard 1. Results obtained for 1976 are summarized in Table 22. In this table, percentage parasitism has been calculated from two different data sets. In each case, real and apparent rates of parasitism are determined. Real parasitism is calculated as percentage of nondegenerated eggs because on occasion parasite larvae was observed in degenerated eggs. An average estimate of real parasitism was 25, 47.3, and 44.7, respectively, for orchards 1, 2, and 3. The percentage parasitism in individual samples from these studies varied between 0 and 100%.

Source of Information	Orchard	% Eggs Degenerated	Parasitism as % of Total Eggs Counted	Parasitism as % of Nondegenerated Eggs Counted <sup>a</sup>
	1	30.0	15.0	21.4
Tables	2	0.0	41.1	41.1
	3	39.1	30.9	50.8
	1	23.3	19.1	25.0
Section IV	2	21.6	37.1	47.3
	3	33.5	29.7	44.7

Table 22.--Comparison of mortality and rate of parasitism by <u>A</u>. <u>epos</u> on overwintering eggs of the white apple leafhopper when egg development was completed.

<sup>a</sup>It is assumed that parasitised eggs were also degenerated, and this is actual rate of parasitism.

## Nymphal-Adult Parasitoid of the WALH

Study of this parasitoid was limited to rearing, identification, and phenological experiments while it was associated with the adult WALH. Results are presented in Tables 6, 8, and 10 and Figures 2, 4, and 6. Association of parasitoid larvae with the host was highest before the host adult WALH population actually peaked. The range of parasitism observed at different sampling dates varied between 0 and 7.14%. Details of the biology of this species were investigated by Steiner (1936) in New York. He reported that adult parasitoids emerged in the first generation in synchrony with WALH nymph emergence and in the second generation slightly sooner than WALH nymph emergence. He reported maximum 78% parasitism in orchards not cultivated when parasitoid cocoons were in the soil. Synchronized emergence of the adult parasitoid with WALH nymphs observed herein and the continuous association of parasitoid larvae with the adult stage of host suggest that this parasitoid is closely synchronized with this pest.

Estimates of parasitism rate in this study were low in comparison to Steiner's (1936) report. Observation taken during this study in other orchards revealed this species is relatively more common than shown in orchards 1-3. During sampling by sweeping nets, maximum rates of parasitism recorded were estimated to be 40.2% in these orchards. In commercial orchards having been exposed to only limited pesticide application, mummified parasitised leafhoppers were found in large numbers on suckers and hanging branches

close to the tree trunk. These estimates were taken by other means and under different conditions and can not be compared with the density estimates taken from orchards 1-3. However, this is evidence that this parasitoid is synchronized with the WALH and it causes substantial mortality. We conclude that protection of this natural enemy should be included in any management program for the WALH.

#### Conclusion

The WALH has two discrete generations in Michigan, but slight overlap is present between late females of the first generation and early males of the second. The WALH overwinters in the egg stage. Development of these eggs starts in late April or early May and egg hatch starts in the first 3 weeks of May. Duration of nymphal period was estimated in 1974 to be 26 days. Adult populations appear during the first 2 weeks of June. Male activity is earlier than female, but longevity of females is longer than that of males. Female activity ends in early August. Considering that postoviposition period of females lasts for an average of 6 days (Armstrong, 1936), it appears that oviposition by the female population of this generation is ended in late July.

In this study, yellow sticky board traps proved to be an efficient tool for obtaining relative density estimates of WALH adult populations and for determination of seasonal phenology of this species. A best absolute density estimate of the adult population can be obtained from the last instar exuvia which remain affixed to the apple leaves for considerable time.

Summer eggs of the WALH occurred in the petiole, main midrib under the surface of the leaves, and in large veins, and direct observations of these eqgs are extremely difficult. Two alternative sampling techniques were found useful for direct observations of WALH eggs: (1) Leaves are bleached in 75% ethanol for 24 hours, washed clean, submerged in a petridish of water, and observed under binocular microscope. (2) Leaves are kept for 1 hour in  $-5^{\circ}$  C, then removed from freezer; while leaves are thawing they were dissected and eqgs counted. The first method is particularly efficient in sampling eggs that are partially or fully developed. This is because of the change from a semi-transparent stage, which is undetectable, to a milky color and later to the red eyed stage, both of which are readily observable. The second method is difficult to use, but eggs are detectable at all stages. This method revealed (in addition to previous oviposition sites mentioned) that many eggs are laid in the midrib on the surface of the leaves. Development of summer eggs was studied with the first method. Eggs in the red eye stage began to appear during the second half of July and peaked in the first half of August. Egg development and nymph emergence in the second summer generation are slower than the first generation. This is due to greater natural variation in the second WALH generation.

Populations of second generation adults appeared from the second week of August and continued to increase until late September. Males became active sooner than females and usually only male populations completed their entire adult life spans. Female populations

in more northern-located orchards were confronted with killing frosts and suffered different levels of mortality.

These data are consistent with the findings of other investigators (Ackerman & Isely, 1931; Armstrong, 1936) relative to insectary rearing programs and field observations. However, there is 2-3 weeks variation in the start and end of activities for these different localities on a geographical basis. This variation can be accounted for in relation to different physical environmental factors in each region, especially in relation to temperature. Information presented here on a calendar basis is discussed in Section III on physiological time scale, and further recommendations for control programs are made.

In this study, four factors--(1) egg parasitism, (2) degeneration of eggs, (3) nymphal-adult parasitism, and (4) cold temperature mortality in fall to second generation adults--were the most significant factors influencing the population dynamics of the WALH in Michigan.

The egg parasitoid, <u>An</u>. <u>epos</u>, overwinters as a larva in the overwintering eggs of WALH. Larvae in overwintering eggs give rise to adult parasitoids which emerge in three discrete periods of time during the growing season. The first group emerges in spring in synchrony with the development and hatch of the overwintering WALH eggs. We hypothesized that this parasitoid population parasitises other alternate host populations available at the time. The second group of parasitoids emerged in synchrony with the first generation

of WALH, but parasitism of eggs was not high, possibly due to difficulty in finding low-density populations or due to the position of the eggs in the host plant. Further research on this interaction phase is recommended. Because of the almost mandatory application of pesticide in commercial orchards during this time period, the management of this pulse of parasitoid activity in current pest management programs is not practical. The third group of parasitoids emerges in synchrony with the oviposition period of second generation WALH in late summer. At this time of the year, the application of pesticides in apple orchards is ended. This provides the most promising biological window for the activity and management of this parasitoid. Therefore, any means to increase the efficiency of this parasitoid during this period is recommended. Also, the highest mortality by this parasitoid as observed in those studies occurred at this time on overwintering eggs. Average real parasitism on overwintering eggs varied between 25 and 47.3%. The reasons for this high level of parasitism are related to: (1) good temporal synchronization between the parasite and host, (2) common spatial coincidence between parasitoid and host, and (3) the density-dependent searching behavior of the parasitoid during this phase of interaction (see Section IV for cases 2 and 3).

In addition to those features, it is hypothesized that dispersal of <u>An. epos</u> from alternative hosts may offer considerable potential for manipulation and increasing the control potential of this species on the WALH. This egg parasitoid was reared from grape

leafhopper eggs on grape leaves in apple orchards and from overwintering eggs of <u>E</u>. <u>maligna</u> on apple. Emergence of the egg parasitoid from the grape leafhopper eggs extends up to the time of the oviposition period of second generation WALH adults. Therefore, study of the extent of dispersal of this parasitoid from grape to apple is recommended. Dispersal study of this parasitoid from other alternative hosts should not be ignored. However, since wild grape is very common in Michigan apple orchards, its study and management seem to be a more feasible alternative host for a leafhopper and <u>An. epos</u>.

The number of generations of <u>An</u>.<u>epos</u> in Michigan is not known. Parasitoid generations emerging from WALH overwintering eggs need to be studied in more detail. Parasitoid emergence in spring should be studied relative to pesticide use so as to maximize their effect on later generations. Furthermore, in commercial orchards, it is probable that parasitoids emerging in the third period (late August-September) are confronted with limited host eggs. Orchards' chemical programs in the second generation should be managed so as to allow early nymphs to emerge in this generation. Their development to adults may provide adequate host eggs for early emerging parasitoids to attack.

Degeneration of overwintering WALH eggs ranged from 21.6 to 33.5% in these studies. It is speculated that growth characteristics of the plant, differential effect of low temperature during egg development, nonfertilization of eggs, or parasitization of partially

developed eggs may account for this condition. In orchard 3, mortality of WALH eggs due to degeneration and parasitism was 78.2%. This mortality reduced the population of WALH to a very low level in the first generation, but they subsequently increased in the second generation.

The nymphal-adult parasitoid, <u>Ap</u>. <u>typhlocyba</u>, is well synchronized to biology of the WALH. It appears to have two generations in Michigan. The maximum apparent parasitism recorded in this study was 40.2%. To our current knowledge, only the pupal stage of this parasitoid can be conserved to enhance the efficiency of this species. Cocoons of this parasitoid occur in the soil, and they are more concentrated under the interior foliage portion of the tree. Research is necessary to determine distribution of these cocoons in the ground cover under the canopy. More study is needed on how to better conserve and manipulate this form relative to cultivation practices, and how to protect other stages of this parasitoid against pesticides. Steiner (1938) discussed this subject, but under current pest management practices his recommendations should be revised.

In more northern counties of Michigan, early frost in fall is a limiting factor for female WALH to complete their activity. Possibly this is another factor in addition to degeneration of eggs and parasitised eggs that usually prevents WALH's from being economically harmful pests in the first generation in Michigan apple orchards.

### SECTION III

# PHENOLOGY OF THE WALH AND ITS EGG AND NYMPHAL-ADULT PARASITOID RELATIVE TO ENVIRONMENTAL TEMPERATURE

### Material and Methods

# Estimation of Minimum Thermal Threshold

The minimum thermal threshold of an organism is that temperature where its development is significantly decreased or stops when exposed to a decreasing array of constant temperature. Appropriate estimation of this value is useful in studying the phenology of an organism based on a linear heat unit or degree day summation approach. This threshold value can be estimated by rearing the organism under different temperature regimes (Morris & Fulton, 1970). It can also be estimated from field-collected data (Arnold, 1959). The latter author gave three methods for estimating the minimum thermal threshold. Although his examples were for plants, the mathematical principles are the same. Two of these methods, including the so-called "least variability method" and the "x intercept method," were used in this study. Data sources employed in this section were those on the phenology of the WALH and its natural enemies, as discussed in Section II. In addition, two data sets on nymphal maturity of T. pomaria were obtained from the literature

(Ackerman & Isely, 1931). Sources of weather data used in this analysis are given for each orchard and year in Table 23.

The "least variability method" was used to estimate the minimum thermal threshold for overwintering egg development. Dates which 50% of the WALH eggs developed to the red eye developmental stage were taken from Tables 1, 2, and 3, respectively, for orchards 1, 2, and 3 in 1976 (Section II). Maximum-minimum temperatures used were from daily averages for each orchard taken from a nearby weather station (Table 23). Base temperatures over the range of 45-55 at intervals of 1° F were evaluated with respect to average daily temperature for each orchard. Degree days above each base temperature were summed from January 1 until 50% of the eggs developed to the red eye stage. Degree day summations at each base temperature in the selected range were averaged for orchards 1, 2, and 3--1976, and coefficient of variation determined. The base temperature with the lowest coefficient of variation was assumed to be the proper base temperature for overwintering egg development. Other data comparisons for 50% egg development and hatch for different years and using degree day summation starting with January 1 or April 1 were also evaluated relative to a coefficient of variation.

The "least variability method" also was used to estimate the minimum thermal threshold for nymphal maturation. Data analyzed were obtained from two different sources. Ackerman and Isely (1931) reported 19.8 and 21.1 days for nymphal maturation, respectively, in average temperatures of 72.3 and 70.5° F. These data were

Table 23;	Source of we to environme	ather data used for correlatic ntal temperature.	n of phenology of <u>T</u> . <u>pomaria</u>
Orchard	Year	January-March and September 16-January <sup>a</sup>	April-September 15
-	1974	Greenville 2 NNE	Recorded for codling moth by H. Riedl
-	1975	=	Belding <sup>b</sup>
-	1976	Ξ	Belding <sup>b</sup>
2	1976	Kalamazoo State Hospital	Kalamazoo State Hospital <sup>a</sup>
m	1976	Grand Rapids WSO	Graham Station <sup>b</sup>
ĸ	1977	-	Graham Station <sup>b</sup>

<sup>a</sup>National Oceanic and Atmospheric Administration.

<sup>b</sup>Michigan agricultural weather station.

obtained under insectary conditions. Data presented in Section II of this dissertation suggest that the duration between 50% nymph emergence and 50% exuvia accumulation was 26 days in orchard 1 (Table 5) and the duration between 20% overwintering WALH egg hatch and 20% adult WALH catch in the first generation was 35 days for both orchard 1 (Tables 1 and 7) and orchard 3 (Tables 3 and 9) 1976. Estimated average temperatures during the nymphal maturation period were 63.75° F for orchard 1--1974 and 62.77 and 62.97, respectively, for orchards 1 and 3 in 1976. In this analysis, degree day summations for nymphal maturation were calculated by subtracting each base temperature over range of 45-55 from the average temperature observed during the nymphal maturation period. The values obtained were multiplied by the duration of nymphal development in days for each orchard data set. The total degree days above the selected range of possible threshold for each base temperature were calculated. Summation of degree days for each base temperature was averaged for the five mentioned data sets and the coefficient of variation calculated for each base temperature. Since pesticides may have influenced adult WALH trap catch in orchard 3, these data were dropped and the coefficients of variation also were recalculated for the four remaining orchards.

The minimum thermal threshold for nymphal maturation was also estimated by "x intercept method," as suggested by Arnold (1959). The percentage rate of nymphal development was calculated from the relationship of  $\frac{1 \times 100}{\text{nymphal duration period in days}}$ . Mean temperature

was used as the independent variable and rate of development as the dependent variable for regression analysis. The  $\underline{x}$  intercept was used as another possible estimate of the minimum thermal threshold. These data were also analyzed when orchard 3 was included and when it was excluded.

# Phenology of the WALH in Relation to Degree Day Summations

Degree day summations above the accepted base temperature were calculated according to sine curve relationship, as suggested by Baskerville and Emin (1969) for each experimental orchard with summation beginning on January 1. Data for percentage overwintering egg development and hatch for orchards 1 and 3 in 1976 (Tables 1 and 3) and orchard 3--1977 (Table 4), and male and female trap catch in first generation and male trap catch in second generation for orchard 1 in 1975 and 1976 (Tables 7 and 9), were compared as cumulative percentages. Data for summer egg development in 1975-1976 were also available (Tables 14 and 15). Modifications of methods suggested by Southwood (1966) and Ruesink (1975) were used for estimation of cumulative development of summer eggs as follows:

$$Ax = \frac{d(N + N-1)}{2}$$

where Ax = area under the curve for two continuous samples, N = numberof eggs in red eye stage counted in later sample, N-1 = number of eggs in red eye stage counted in previous sample, and d = differences in degree days accumulated between two continuous samples. Surface areas calculated between each two samplings were pooled for all sampling periods. Total surface area under the density curve was calculated and cumulative percentage for each sampling date was estimated for the development of summer WALH eggs to the red eye stage.

The above data were plotted on a degree day summation scale for graphical interpretations and to evaluate base temperature estimates. Because of the sigmoid distribution of data, percentage development and activity (dependent variables) were transformed to probit by reading the values for each cumulative percentage from tables given by Finney (1952). Regression lines for rate of development and WALH activity were calculated by using probit of rates as dependent variables and degree day summations as the independent variable.

No complete data on WALH egg hatch during the summer or for female activity in the second generation were collected in this study. It was assumed that degree day requirements from egg development to egg hatch would be the same for both generations. Also, it was assumed that the degree day requirements between the start of male adult activity and female adults would be the same for both generations. These values for the first generation were calculated from regression line estimates. Therefore, nymph emergence from summer eggs was predicted from summer egg developmental curve by adding the additional degree days equivalent to the first generation. Female adult activity was predicted from second generation male activity

curves by the addition of the appropriate degree days equivalent noted in the first generation. Probit values for a total of six estimated and two predicted regression lines were retransformed to percentages. Average developmental and activity curves were plotted and actual data points marked for comparison of actual data (Figure 21). Since the beginning and peak or 50% activity of these variables are important timing events in pest management programs, degree days for probit 3 and 5 as representative of 2 and 50% development and activity were calculated from the regression lines.

### Phenology of Parasitoids in Relation to Degree Day Summations by the WALH

Data on development and activity of the egg parasitoid <u>An</u>. epos and the nymphal-adult parasitoid <u>Ap.typhlocyba</u> were too incomplete to carry out a similar detailed analysis as was done for the WALH. Since both natural enemies are well synchronized with the WALH (Section II), it was expected that the development and activity of the host would have had a significant influence on the activity of these natural enemies. Therefore, the range of activity of the adult <u>An</u>. epos for orchards 1 and 3, 1976, and range of association of parasitoid larvae of <u>Ap.typhlocyba</u> with WALH adults for orchard 1 in 1975 and 1976 were calculated according to degree days accumulated by the host. Adult <u>Ap.typhlocyba</u> are known to emerge in close synchrony with WALH nymphs in both generations (Steiner, 1938). Therefore, the initial activity of the WALH nymphal emergence was related to the start of Ap. typhlocyba adult activity in both generations.
# Result and Discussion

### Estimation of Minimum Thermal Threshold

Estimation of the lowest coefficient of variation for degree days accumulated to 50% egg development in orchards 1, 2, and 3 in 1976 is plotted in Figure 15. The minimum coefficient of variation occurred at base temperature 48° F. Other data comparisons by adding data from different years or using alternative degree day summations starting with April 1 did not add any meaningful information to this estimate. Since an estimate of base temperature 48° F was determined to be the least variable value for the same year, preliminarily it was accepted as the best base temperature for overwintering egg development. When the "least variability method" was used to estimate minimum thermal threshold for nymph maturation, the lowest coefficient of variation occurred at a base temperature of 49.5° F, when data from orchard 3 were included in the analysis. When data from orchard 3 were excluded, the best base temperature was 48° F (Figure 16). For the same data set, but using the "x intercept method," the minimum thermal threshold was estimated to be 48.4 when data from orchard 3 were included, but it was estimated to be 46.4 when data from orchard 3 were excluded (Figure 17).

From these analyses, the range of 46.4-49.5° F probably includes the minimum thermal threshold for overwintering eggs and nymphal development of the WALH. Arnold (1959) suggested that plus or minus one or two degrees error in estimating of base temperature



Figure 15.--Coefficient of variation in degree days at various base temperatures for <u>T</u>. <u>pomaria</u> overwintering egg development, orchards 1, 2, 3, 1976.



Figure 16.--Coefficient of variation in degree days at various base temperatures for  $\underline{T}$ . <u>pomaria</u> nymph maturation. For data source, see text.



was not critical. Also, error on the upper side of the range is more serious than on the lower side of the base. This is well verified in Figures 15 and 16. Since base temperature of 48° F was estimated as the minimum thermal threshold of overwintering eggs, it was used as the threshold for all further analysis presented herein. When data were plotted versus degree day summations above 48° F, they were biologically meaningful (Figures 18 and 19). This base temperature, however, can certainly be improved upon in terms of accuracy in the future. Also, it may not be correct for more southernly located populations of the WALH. This is indicated by the reports of a much longer incubation period for summer eggs of the WALH in the southern states of the United States in comparison to northern states (see literature review).

#### <u>Phenology of the WALH in Relation</u> to Environmental Temperature

Regression lines for the phenology of the various stages of the WALH are presented in Figure 20. Solid lines represent development and activity estimates from original data; broken lines are predicted values for egg hatch during summer and female activity in the second generation. Average cumulative development and activity curves are given in Figure 21. Points on the curves in Figure 21 are the actual data shown in comparison to the model. Degree day summations for 2% and 50% development and activity are presented in Table 24. As discussed in Section II, overwintering egg development and hatch are very rapid in comparison to egg development during the











Figure 20.--Average regression lines for probit transformed data for egg development, hatch, male and female activity of  $\underline{I}$ . <u>pomaria</u>.



that parasitised leafhoppers were detected



summer. The same relationship is expected for adult activity between the first and second generation. The actual data observed for these events, however, did not show such a relationship. Regression lines for adult activity in the second generation were very steep. This was a result of killing frosts which prevented the adult populations from completing their entire life span in this generation. On the basis of complete survival of this generation, an expected population curve for adult activity in the second generation was constructed (Figures 20 and 21). Additional research is needed to verify the accuracy of these estimates.

Table 24.--Degree day summation from January 1 for 2% and 50% development and activity of different stages of the T. pomaria.

Generation	Stage	2%	50%
	Egg development	227.7	338.8
<b>F 1</b>	Egg hatch	315.8	425.6
First	Male activity	582.3	956.7
	Female activity	724.2	1,280.7
	Egg development	1,515.4	1,880.6
Second	Egg hatch	1,603.0	1,966.9
	Male activity	2,231.8	2,631.7
	Female activity	2,373.0	2,955.2

In general, the model for the development of the WALH described herein gives a reasonably accurate representation of the data collected during the course of this study. However, other biological parameters such as maximum thermal threshold, humidity, and photoperiod effects are not included. These may be useful in improving the model in the future. This research, along with additional developmental data and more validation experiments, would enable one to develop a more refined model of the phenology of this pest. Such research is necessary before a WALH system could be included in the PETE (predictive estimate timing estimators) system used in Michigan for integrated pest management (Welch et al., 1978).

# Phenology of Parasitoids in Relation to Degree Day Summation by the WALH

The range of activity for the adult <u>An</u>. <u>epos</u> for orchards 1 and 3, 1976, is summarized in Table 25. These data are shown as horizontal bars on the 50% region in Figure 21. Comparison with WALH curves suggests synchronization of <u>An</u>. <u>epos</u> adults with WALH eggs. Actual oviposition trends of the WALH were not measured, but considering the preoviposition period and activity curves of female WALH, this synchronization is expected to be good.

The range of degree days that the <u>Ap</u>.<u>typhlocyba</u> larvae were associated with the WALH is given in Table 25 for orchard 1, 1975 and 1976. These periods are shown on Figure 21 as horizontal bars at the 70% region. Broken lines in front of the solid lines are estimates of adult <u>Ap</u>.<u>typhlocyba</u> activity. This is just before parasitised leafhoppers can be detected in the orchard.

	Peri	od 1	Perio	d 2	Perio	od 3
	Start	End	Start	End	Start	End
Orchard 1, 1976	245	552.5	1,001.5	1,462	2,561	?
Orchard 3, 1976	261	599.5	1,004.0	1,468	2,571	?
Range	245 -	599.5	1,001.5	- 1,468	2,561	-

Table 25.--Degree day summations above  $48^{\circ}$  F from January 1 relative to activity of <u>A</u>. <u>epos</u> (part A) and <u>A</u>. <u>typhlocyba</u> (part B).

	First Ger	neration	Second (	Generation
	Start	End	Start	End
Orchard 1, 1975	885.0	1,416	2,413	2,781.5
Orchard 1, 1976	945.5	1,303	2,488	2,877.0
Range	885.0 -	1,416	2,413 -	- 2,877.0

### Conclusion

A range of 46.4-49.5° F probably includes the minimum threshold temperature for development of overwintering eggs and nymphs of the WALH. A base temperature of 48° F was the mean estimate and least variable value. It was used as a common base temperature to evaluate the development and activity of the different stages of the WALH. While this value proved to be appropriate for Michigan populations, higher or lower values for more southernly populations may be expected, based on literature reports.

A phenology model relative to environmental temperature was developed for estimating egg development, egg hatch, and the activity of different sexes of adult WALHs in both generations. The model mimicked natural population events for most life stages, but for late season activity of WALH adults in the second generation there were some observed discrepancies. Also presented is range of activity for <u>An</u>. <u>epos</u> and <u>Ap</u>. <u>typhlocyba</u> relative to thermal threshold and degree day summation for the WALH.

When refined, the model discussed herein will be useful for decision making and prediction for WALH management. If high overwintering populations are present, spray applications are necessary for control of the WALH in the first generation. Advanced prediction of nymph emergence would be helpful for growers. According to the model, a pest manager could start sampling overwintering eggs up to 200° D (base 48° F) after January 1. If percentage eggs developed to red eye stage could be estimated as a reference point, a more

precise forecast of egg hatch could be made in advance of egg hatch. In general, chemical control programs at this time should be made on the basis of maximizing mortality of the WALH and minimizing mortality of its natural enemies. Delaying sprays until egg hatch is completed should increase survival of An.epos early in the season. On a degree day basis, this period would be 245-600° D above 48° F from January 1. This delay for applying pesticides will probably be made on the basis of the entire pest complex present in an apple orchard. However, relative to the WALH alone, a delay in spraying in the first generation is not so critical because (a) egg hatch is very rapid; (b) before adults are active, egg hatch is almost completed and the majority of nymphs are in the early susceptible stage of development; and (c) the earliest nymphs will be males, which pose no direct threat to the next generation. Delayed spraying would also cause immature females to suffer higher mortality. Therefore, if a spray application is only for control of the WALH, the egg parasitoids that directly interact with the WALH could readily be protected by such action. However, if An.epos were interacting with other alternative hosts in the same apple orchard, the timing situation for chemical control may be more complicated.

Protection of <u>Ap</u>. <u>typhlocyba</u> in the first WALH generation is more difficult as compared to <u>An</u>. <u>epos</u>. As shown in Figure 21, this parasitoid throughout its life is probably directly or indirectly subjected to all pesticides influencing the WALH host. However, spray programs can be adjusted ecologically to minimize the effect

of pesticides on this natural enemy. This may be achieved with delay in pesticide application to conserve the males of the WALH at levels causing no significant damage but killing the predominantly female WALH population (see also Steiner, 1938). Such tactics would allow for partial Ap. typhlocyba survival in apple orchards.

Emergence of the second pulse of <u>An</u>. <u>epos</u> from overwintering eggs is between 1,001.5-1,468° D above 48° F from January 1. This is in synchrony with the initial oviposition of WALH summer eggs. No pesticides usually are applied for leafhopper control during this time period because pesticides are relatively ineffective on adults. However, spray programs against other pests may affect <u>An</u>. <u>epos</u> at this time. Since the specific interactions of this parasitoid group with summer eggs of the WALH are unknown, few recommendations relative to these populations can be made at this time. However, protection of these parasitoids whenever possible is recommended and further research in this phase of interaction should be conducted in the future.

Recommendations for spraying for control of second generation WALH can be predicted by sampling summer egg population after 1,400° D (base temperature 48° F). Observations of first eggs in the red eye stage could be used as a reference point to predict nymph emergence from summer eggs more precisely. Emergence of nymphs from summer eggs occurs over a wider time span than from overwintering eggs. Similar to the first generation, early nymphs first give rise to a male population, which does not contribute eggs to the next generation.

However, male population densities in the second generation more often can be high enough to cause significant foliage damage in orchards. Slow nymphal emergence from summer eggs, corresponding with the end of female oviposition activity in the previous generation, can provide another management window for control of the WALH. This area is in need of further research. A dual sampling of nymphs and eqgs in the early period of nymph emergence could provide a pest population estimate in the summer generation. With the knowledge of this density and an appropriate threshold value, the necessity of spraying could be estimated. This approach would require improved methods for egg sampling; also current estimates for the economic threshold of the WALH are relatively poor and mostly based on empirical data (Garman & Townsend, 1936). They would require further study also. An alternative to this approach is more precise sampling of early emerged nymphs and interpolation of the total WALH population density from eqg hatch curves. Needed for this approach is an improved and fully validated phenology model for the WALH.

Conservation of egg parasitoid,  $\underline{An} \cdot \underline{epos}$ , during the period in which summer eggs are hatching is not very critical. However, protection of early WALH nymph individuals that give rise to female WALH for deposition of early overwintering eggs may be critical to provide host material for the third pulse of parasitoid that emerges from overwintering eggs. This would not be an easy management tactic to carry out, because early nymph individuals are expected to be males and a long delay in pesticide application may cause significant

damage by this pest. Again, protection of <u>Ap</u>. <u>typhlocyba</u> could better be achieved by a delay in spray application early in the nymph emergence period. Late season WALH adults parasitised by <u>Ap</u>. <u>typhlocyba</u> may be subjected to late season mortality by frost similar to their host, as will be discussed later. Generally, it is anticipated that any delay in spray application after nymphal emergence should result in higher survival of <u>Ap</u>. <u>typhlocyba</u>.

The observed data versus the phenology model prediction suggested that female population in the second generation suffered 52% mortality in late season when it was exposed to colder temperature condition (see Figure 21). Data presented in Tables 7 and 9 (Section II) suggest that some females still were present in the orchard some 6 weeks after peak female activity in the first generation. However, in the second generation this only lasted for 2 weeks due to the cold-induced mortalities. The predicted value for female activity shown in Figure 21 could be in considerable error due to: (1) The width or level of variation within the emergence of a population in subsequent generation within the same year should increase due to compounded natural variation from generation to generation. Cumulative percentage curves should therefore be flattened in subsequent generations. This fact, when compared with the female activity curve of Figure 21, suggests that an underestimated prediction of mortality was made. (2) Another complicating factor is that minimum thermal threshold for adult activity of a species is usually higher than the value for development. During the second

generation, the average temperature during the period of actual activity was lower in comparison to activity period of adults in the first generation. This could have reduced the trap catch appreciably in the second generation and significantly affected activity curves. In this case, predicted mortality could be overestimated. Further research is needed to estimate the threshold of cold temperature on the WALH adults and the magnitude of mortality inflicted in this stage in normal seasons. With such data, the maximum population potential could be estimated for the next season spring generation in different geographical areas relative to population densities and temperature information.

#### SECTION IV

SPATIAL DISTRIBUTION OF OVERWINTERING AND SUMMER EGGS OF THE WALH AND THE COINCIDENCE OF PARASITISM BY <u>AN. EPOS</u> TO THE DISTRIBUTION OF ITS HOST

#### Material and Methods

## Distribution of Overwintering Eggs of the WALH on the Apple Branches and Coincidence of Parasitism by An. epos

In orchard 1--1974, six Red Delicious apple trees were randomly selected. Each tree was divided into three zones (upper part, lower part outside, and lower part inside), and each zone was divided into quadrants (north, west, south, and east). In each quadrant one branch was sampled randomly. Each branch was accepted in the sample if it had at least five spur buds to assure maximum oviposition of the WALH as reported by Armstrong (1936). The maximum age of branches sampled was 9 growing seasons old. In this orchard, two samples were taken: (1) before overwintering egg development started (5/6/74) and (2) after egg hatch was completed from overwintering eggs (6/19/74). In addition to these samples, at the first sampling date a similar sample was taken from a commercial apple block (Klacle orchard) in the vicinity of orchard 1. Each branch sampled was divided into subsamples according to number of spur buds on each branch. A 5 cm length section of each subsample was selected, and

the total number of overwintering eggs and parasitised eggs counted on each subsample (characteristics used to determine eggs and parasitised eggs were as described in Section II). Total counts for each specific age of branch and each sampling date were pooled to determine the distribution of overwintering eggs and parasitised eggs of the WALH. According to the distributional pattern of the WALH, an appropriate sample unit was selected (see result and discussion). Observations in the Klacle orchard and later observations in orchard 1 suggested that establishment of a sample unit according to the age of the branch was not practical.

In 1976, the average growth length of branches for several sequential growing seasons was estimated in orchards 1, 2, 3, and another candidate orchard for this study. A 15 cm length of branch was estimated to be equivalent to the annual branch growth rate. Data on WALH and parasitoid distribution and densities were recorded on every 15 cm interval of branches 75 cm or longer. Two objectives were involved in this research phase: (1) Study of development, hatch, and mortality of WALH's overwintering eggs (see Section (2) Study of spatial distribution of overwintering eggs on II). the branches. For both objectives, samples and sampling plan were the same as described in Section II, and variables were counted on every 15 cm of a 75 cm or longer branch. The problem was establishment of a standard sample unit and transforming the earlier collected data to a common standard. Therefore, distribution of overwintering eggs was determined from these data by pooling several

sampling dates (Tables 1, 2, and 3, Section II). A length of branch with the highest density of overwintering eggs and least variability for population counts was selected as the sample unit. All data previously collected were recalculated according to this sample unit, and thereafter this sample unit was used.

### Inter- and Intratree Distribution of WALH Eggs and Coincidence of Parasitism by An. epos

In orchards 1, 2, and 3, 1976, six trees were sampled randomly. Each tree was stratified into two levels (upper part and lower part) and each level divided into quadrants (north, south, west, and east). In each quadrant two branches were sampled. The length of each branch was limited to a minimum of 75 cm length or longer. The 15 cm apical section of the branch and part of the branch beyond the 75 cm length were discarded, because of lower egg density and high count variability (see result and discussion). On the remaining branch, two subsamples were taken. Each subsample was  $25 \text{ cm}^2$ , which did not overlap. Each subsample was determined by estimating the diameter of the subsample by a calipter at 0.5 mm accuracy and then determining its length from the relation  $L = \frac{S}{\pi n}$ , where S = selected surface area, D = measured diameter, and  $\pi$  = 3.14 constant (branch is assumed to be a perfect cylinder). On each subsample, the total number of eggs, number of parasitised eggs, and number of degenerated eggs were counted.

To determine within-tree distribution of summer eggs in orchard 1, in 1975 14 Ida Red apple trees and in 1976 6 trees of mixed varieties of apple were randomly selected and stratified in the same manner as for the study of overwintering eggs. However, the sample unit was a leaf and 10 leaves were sampled per quadrant. Samples were taken during the oviposition period of the first generation WALH adults and during egg developmental period at weekly intervals. Leaves were treated with ethanol bleaching technique as described in Section II. In 1977, these observations were repeated in an unsprayed, commercial apple block in lower south-east Michigan (Wasem orchard), but only three samples were taken during the egg developmental period at 2-week intervals.

## Result and Discussion

## Distribution of Overwintering Eggs of the WALH on the Apple Branches and Coincidence of Parasitism by An. epos

Data on spatial distribution for total and parasitised overwintering eggs of the WALH for orchard 1, 1974, are presented in Table 26 and Figures 22 and 23. The highest egg density of WALH's overwintering eggs was found on 3- to 4-year-old wood of apple branches. The distribution of parasitised eggs closely followed the distribution of the host eggs. Since as the wood age classes increased surface area increased, calculated means in Table 26 probably underestimated leafhoppers and parasitoid densities for very small branches and overestimated them for older branches. Data suggested that the youngest branches were more suitable sites than older branches for oviposition site of the WALH. Since growers are interested in

Variable and			Age of Bran	ich (Growing Se	sasons 01d)	
Sampling Date	Statistic	-	2	3	4	5
)verwintering eggs 5/6/74	<u>X</u> ± S/√n	0.166±0.090	0.500±0.145	1.222±0.267	1.111±0.214	<b>0.944±0.14</b> 1
)verwintering eggs 6/19/74	<u>X</u> ± S/√n	0.027±0.019	0.305±0.110	0.847±0.152	1.194±0.158	1.013±0.189
Parasitised overwintering eggs 6/19/74	<u>X</u> ± S//n	0 +	0.111±0.046	<b>0.250±0.058</b>	0.527±0.108	0.500±0.121

 $\overline{X} \pm S/n = mean \pm standard error.$ 







Figure 23.--Distribution of proportion of total eggs and parasitised eggs of <u>T</u>. pomaria overwintering population on 1-5 growing seasons old branches, orchard 1, 1974.

maintaining vigorous 1-4 growing wood to guarantee maximum fruit production, a sample unit including the previous four growing seasons' branches would contain a high proportion of the overwintering WALH population available in the orchard. Although many eggs may occur on older branches, densities are low, counts show high variability, and practical sampling limitations restrict them from inclusion in a sample unit.

Although the establishment of a sample unit based on equal lengths of five sequential growing seasons was deemed to be the best sample unit, data collected in Klacle orchard in 1974 and later observations indicated it to be an impractical one in certain cases. For example, in abandoned orchards annual growth length is irregular and usually growth is too short to provide meaningful information relative to low leafhopper density. Also, in commercial orchards annual growth is very rapid and 1- or 2-year-old branches may be very long and thick enough to provide suitable oviposition sites for the WALH. For these reasons it was hypothesized that there usually is a better correlation between WALH egg densities and the diameter and thickness of the apple branches.

Results for 1976 to test this hypothesis are presented in Table 27 and Figure 24. Considering the differences observed in means and the associated degree of precision of these counts, a 75 cm apical part of a branch is an appropriate sample unit for relative estimates of overwintering WALH population. Such a sample unit was used for study of the seasonal development of the overwintering eggs

from apical part	of the branch	1976.				
		Distance	From Apical	of Branch (	in cm)	
	0-15	15-30	30-45	45-60	60-75	75-90
Orchard 1						
Sample size	60	60	60	60	60	44
Mean ± standard error	0.03±0.02	0.71±0.17	1.01±0.17	1.21±0.23	1.18±0.20	0.63±0.21
Orchard 2						
Sample size	80	80	80	80	80	17
Mean ± standard error	0.01±0.01	0.07±0.03	0.25±0.08	0.47±0.11	0.60±0.10	0.62±0.14
Orchard 3						
Sample size	60	60	60	60	60	44
Mean ± standard error	0.08±0.03	0.75±0.17	2.32±0.36	3.07±0.61	<b>4.4</b> 3±0.66	<b>4.07±0.8</b> ]

Table 27.--Mean density differences of <u>T</u>. pomaria overwintering population relative to distance



Figure 24.--Mean density differences of <u>T</u>. <u>pomaria</u> overwintering population relative to distance from apical part of the branch (A) and degree of precision that describes these differences (B).

in Section II. For study of the spatial distribution of the overwintering eggs of the WALH, a more precise sample unit on a surface area basis was used to compare density differences in different sampling sites. Again a 75 cm length of apical part of the branch was selected initially as a sample unit, but this sample unit was subsampled on a surface area basis.

### Inter- and Intratree Distribution of WALH Eggs and Coincidence of Parasitism by An. epos

The distribution of overwintering and parasitised WALH eggs at three different sampling sites in orchard 1--1974 is presented in Figure 25. This distribution pattern indicates that overwintering populations of the WALH are aggregated. To investigate this phenomenon in more detail, the original data collected in 1976 are presented in Appendix B. The  $\chi^2$  test applied to these data sugqested that the distribution of total WALH eggs and parasitised eggs by An. epos was not significantly different from negative binomial distribution (Figure 26). Mean variance and k value (coefficient of negative binomial) for each of these variables and for each experimental orchard are presented in Table 28. The highest k value or least aggregated form of the overwintering population of the WALH was found in orchard 1 ( $\underline{k}$  = 1.5313) and the least  $\underline{k}$  value or more aggregated form for the same variable is found in orchard 2 ( $\underline{k}$  = 0.6670). For orchard 3, the k value (k = 0.7404) was in between the other two orchards, but it was closer to the value found in orchard 2. These differences in aggregation probably are related to different host



Sampling sites

Figure 25.--Distribution of proportion of total eggs and parasitised eggs of <u>T</u>. <u>pomaria</u> overwintering population in different sampling sites, orchard 1, 1974.

	orchards	1, 2, and 3	3, 1976. <sup>-</sup>						=
Orchard	Ē	<u>pomaria</u> Egg Host Plant	uo st	A.	epos in Ha of Host <sup>b</sup>	bitat		. epos on Host <sup>c</sup>	the
	Mean	Variance	الح	Mean	Variance	لم الم	Mean	Variance	ъ Ч
L	1.25	2.48	1.5313	0.24	0.39	0.3537	0.38	0.58	0.7663
7	1.01	2.54	0.6670	0.37	0.93	0.1988	0.82	1.69	0.6921
ю	5.22	63.01	0.7404	1.55	11.79	0.1432	1.89	13.72	0.1880

parameters	epos in
statistical	itised by <u>A</u> .
k value)	gs paras
inomial (	<u>omaria</u> eg
ent of negative b	<u>pomaria</u> and <u>T. p</u>
, and coeffici	ing eggs of <u>T</u> . and 3, 1976.
, variance	overwinter ards 1, 2,
28Mean	for ( orchi
Table	

<sup>a</sup>Coefficient of negative binomial distribution.

<sup>b</sup>Data with zero host count included.

<sup>C</sup>Data with zero host count excluded.



Figure 26.--Fitting of negative binomial to observed distribution of overwintering eggs of <u>T</u>. <u>pomaria</u> and parasitised eggs by <u>A</u>. <u>epos</u>, orchard <u>3</u>, 1976. Broken line = observed data, solid line = expected.

plant characteristics. Orchard 1 is a completely abandoned orchard with low plant growth rate and a more uniform vegetative growth pattern in comparison to orchards 2 and 3. Orchard 2 is semiabandoned and trees in this orchard are occasionally hedge pruned. The plant growth rate is irregular on each tree. Inside the trees, branches are usually old rugorous branches which are not preferred by WALH, but outside branches have vigorous growth. Orchard 3 is a commercial apple orchard. It was hand pruned to assure highest crop production and the majority of branches are of 1-4 growing seasons old. Plant characteristics in this orchard are more uniform in comparison to orchards 1 and 2, but since it is disturbed habitat for the WALH in terms of pesticide use, interpretation is more difficult.

The <u>k</u> values for parasitised eggs in the host habitat and on available host (when zero host counts were excluded) were highest for orchard 1. This orchard also has the highest <u>k</u> value for the host. In orchards 2 and 3, the <u>k</u> values for the parasite were the least and they were inversely correlated with the <u>k</u> value of the host.

To determine the source of variation for total overwintering eggs and parasitised eggs of the WALH, analysis of variance (ANOVA) procedures were applied after a transformation of data to  $\log_{10} (x + 1)$ (Morris, 1955; Sokal & Rohlf, 1969). Results are presented in Tables 29-34. In each table, sources of variance were tested against residual error.

ANOVA results for total overwintering eggs (Table 29) in orchard 1--1976 showed only a significant source of variation for intertree variance. This source of variation undoubtedly represents density differences on different host trees due to varietal differences (Trammel, 1974). Lack of significance for other sources of variation was expected because of the more uniform growth of the host plant in this orchard, as discussed earlier.

ANOVA results for parasitised eggs in orchard 1--1976 are presented in Table 30. Only intertree variance for parasitised eggs was significant. This would be an expected response of parasitoid closely attuned to the distribution of its host. The proportion of total counts for eggs and parasitised eggs in different sampling sites in orchard 1 is presented in Figure 27. This graphical analysis demonstrates the possible sources of variation, as discussed above.

ANOVA results for orchard 2 are presented in Tables 31 and 32. The only significant source of variance in this orchard was intertree variation. However, comparison of significant levels between orchards 1 and 2 suggests greater variation between levels in orchard 2. In this orchard again intertree variation was expected because of mixed varieties. Variations between levels resulted from higher WALH densities in the upper parts of trees. This was believed to be a response of WALHs to the more extensive vegetative growth in this level. ANOVA results for parasitised eggs in orchard 2 were similar to those for the host, but significance levels differed

Source of Variance	df	Mean Square	Significance of F
Main effects	9	0.100	0.116
Tree	5	0.158	0.032
Quad	3	0.020	0.794
Level	ו	0.050	0.362
2-way interaction	23	0.073	0.258
Tree x quad	15	0.062	0.418
Tree x level	5	0.098	0.161
Quad x level	3	0.086	0.238
3-way interaction	15	0.050	0.617
Explained	47	0.071	0.261
Residual	48	0.059	
Total	95	0.065	

Table 29.--Analysis of variance of inter- and intratree variability in overwintering eggs of  $\underline{T}$ . pomaria, orchard 1, 1976.

Table 30.--Analysis of variance of inter- and intratree variability in parasitised overwintering eggs of  $\underline{T}$ . <u>pomaria</u> by <u>A</u>. <u>epos</u>, orchard 1, 1976.

Source of Variance	df	Mean Square	Significance of F
Main effects	9	0.024	0.334
Tree	5	0.041	0.089
Ouad	3	0.002	0.962
Level	ī	0.000	0.884
2-way interaction	23	0.020	0.508
Tree x guad	15	0.022	0.409
Tree x level	5	0.016	0.568
Quad x level	3	0.017	0.473
3-way interaction	15	0.026	0.242
Explained	47	0.023	0.353
Residual	48	0.020	
Total	95	0.021	



Figure 27.--Distribution of proportion of total eggs and parasitised eggs of overwintering <u>T</u>. <u>pomaria</u> population in different sampling sites in orchard 1, 1976. Letters U, D, W, S, E, N, respectively, stand for upper, lower, west, north, south, and east of the trees. Numbers refer to numbers given to trees.
Source of Variance	df	Mean Square	Significance of F
Main effects	9	0.208	0.005
Tree	5	0.272	0.004
Quad	3	0.101	0.227
Level	1	0.208	0.085
2-way interaction	23	0.038	0.931
Tree x quad	15	0.048	0.754
Tree x İevel	5	0.026	0.858
Quad x level	3	0.007	0.960
3-way interaction	15	0.039	0.881
Explained	47	0.071	0.433
Residual	48	0.067	
Total	95	0.069	

Table 31.--Analysis of variance of inter- and intratree variability in overwintering eggs of  $\underline{T}$ . pomaria, orchard 2, 1976.

Table 32.--Analysis of variance of inter- and intratree variability in parasitised overwintering eggs of  $\underline{T}$ . <u>pomaria</u> by <u>A</u>. <u>epos</u>, orchard 2, 1976.

Source of Variance	df	Mean Square	Significance of F
Main effects	9	0.093	0.016
Tree	5	0.145	0.004
Ouad	3	0.008	0.887
Level	ī	0.094	0.114
2-way interaction	23	0.021	0.922
Tree x guad	15	0.024	0.818
Tree x level	5	0.019	0.747
Quad x level	3	0.010	0.835
3-way interaction	15	0.019	0.909
Explained	47	0.034	0.573
Residual	48	0.036	
Total	95	0.035	



Sampling sites

Figure 28.--Distribution of proportion of total eggs and parasitised eggs of overwintering <u>T</u>. <u>pomaria</u> population in different sampling sites in orchard 2, 1976. Letters U, D, W, N, S, E, respectively, stand for upper, lower, west, north, south, and east of trees. Numbers refer to numbers given to trees. between the two. Total counts for WALH and parasitoids including both level, quadrant, and tree variables in orchard 2 are presented as proportions in Figure 28. These data describe graphically the possible sources of variation as described by the ANOVA.

ANOVA and graphical results of distributional studies for orchard 3 are presented in Tables 33 and 34 and Figure 29. In this orchard, intertree variance and variations between the two levels were highly significant. The same explanation for these results as discussed for orchard 2 best accounts for these differences. In this orchard, variation between quadrants was fairly significant compared to intertree and between-tree levels. But it was highly significant in comparison to variation between quadrants as observed in orchards 1 and 2. This extra source of variation in orchard 3 was not known precisely, but it is likely that more variable management practices had a major influence on this variation. ANOVA results in this orchard for parasitised WALH eggs are similar to results for the host. This is interesting, because in spite of the variable management practices employed, parasitoids were flexible enough to adjust to the altered distribution of its host. This would be expected if the natural enemy was closely tied to the host and was effective. Also during this period of study the effect of pesticides on the parasitoid was minimal.

Comparing results for the three orchards, only intertree variation seemed statistically and biologically significant. The significant variations between levels in orchards 2 and 3 were

Source of Variance	df	Mean Square	Significance of F
Main effects	9	0.675	0.001
Tree	5	0.822	0.001
Quad	3	0.229	0.088
Level	1	1.277	0.001
2-way interaction	23	0.188	0.031
Tree x quad	15	0.183	0.054
Tree x level	5	0.256	0.038
Quad x level	3	0.097	0.411
3-way interaction	15	0.073	0.732
Explained	47	0.245	0.001
Residual	48	0.099	
Total	95	0.171	

Table 33.--Analysis of variance of inter- and intratree variability in overwintering eggs of  $\underline{T}$ . pomaria, orchard 3, 1976.

Table 34.--Analysis of variance of inter- and intratree variability in parasitised overwintering eggs of  $\underline{T}$ . pomaria by <u>A</u>. epos, orchard 3, 1976.

Source of Variance	df	Mean Square	Significance of F
Main effect	9	0.335	0.002
Tree	5	0.482	0.001
Ouad	3	0.102	0.370
Level	ī	0.296	0.084
2-way interaction	23	0.163	0.058
Tree x guad	15	0.219	0.015
Tree x level	5	0.079	0.536
Ouad x level	3	0.026	0.848
3-way interaction	15	0.060	0.839
Explained	47	0.163	0.033
Residual	48	0.095	
Total	95	0.129	



Sampling sites

Figure 29.--Distribution of proportion of total eggs and parasitised eggs of overwintering <u>T</u>. <u>pomaria</u> population in different sampling sites in orchard 3, 1976. Letters U, D, S, W, E, N<sub>2</sub> stand, respectively, for upper, lower, south, west, east, and north of trees. Numbers refer to numbers given to trees. expected in response to the more vigorous vegetative growth in the upper part of the tree. This was mostly the result of management practices, especially pruning. Further sources of variations were expected as a result of a disturbed or managed habitat. Comparative sources of variations were found between parasitised eggs and total WALH eggs. While the response of the WALH to its host plant was expected, the similar results for the parasitoid reflected the close association of this species to the distribution of its host.

Because of significant intertree variation for both the WALH and <u>An</u>. <u>epos</u>, total counts/tree were treated as a single ecological entity. The number of parasitised eggs was considered the dependent variable and total egg counts the independent variable. These data for each orchard were subjected to regression analysis. Similarly, for each individual sample, data for only parasitised eggs were subjected to the same regression analysis. Results are presented in Figures 30-32. The slope of the regression line and amount of correlation show that densities of the WALH and <u>An</u>. <u>epos</u> are positively correlated. This was also relatively indicated by the k values for the WALH and parasite distributions (Table 28). This would indicate that <u>An</u>. <u>epos</u> was more active with highest aggregation of the host and effective in parasitising its host in orchards.

Counts for the spatial distribution study of summer WALH eggs in orchard 1--1975 and 1976 were too low (Tables 14 and 15, Section II) to analyze. Also, as described in Section II, the ethanol bleaching was somewhat inefficient in detecting summer egg



Figure 30.--Response of <u>A</u>. <u>epos</u> to aggregation of overwintering eggs of <u>T</u>. <u>pomaria</u> in orchard 1, 1976. (A) Individual samples when at least one parasitised host detected. (B) Sixteen samples per tree are pooled.



Figure 31.--Response of <u>A</u>. <u>epos</u> to aggregation of overwintering eggs of <u>T</u>. <u>pomaria</u> in orchard 2, 1976. (A) Individual samples when at least one parasitised host detected. (B) Sixteen samples per tree are pooled.



Figure 32.--Response of <u>A</u>. <u>epos</u> to aggregation of overwintering eggs of <u>T</u>. <u>pomaria</u> in orchard 3, 1976. (A) Individual samples when at least one parasitised host detected. (B) Sixteen samples per tree are pooled.

population. Data collected in 8/13/77 in an unsprayed commercial apple block were dense enough for such an analysis. Eggs in the petiols, midribs, and main veins in this orchard were very dense and were counted during the peak period of summer egg development. This count, determined from results presented in Table 17 (Section II), was estimated to underestimate the available WALH population by 34.7% on this date. This error also was a result of deficiency in counting eggs in the veins on the surface of the leaves. The proportional distribution of summer WALH eggs relative to within-tree and betweentree sampling sites is shown in Figure 33. The original data are presented in Appendix B. Data suggest the highest variability was also between trees for summer eggs; however, additional research on this subject is needed.

# Conclusion

Overwintering eggs of the WALH were observed on apple branches of 1-9 growing seasons old. However, the largest proportion of eggs was laid on wood 2-4 growing seasons old. A sample unit of equal length or surface area from wood of 2-4 growing seasons old will sample most of the overwintering population. In practice, this method may have certain limitations due to irregular growth characteristics of branches in different growing seasons. Substitution of a 75 cm apical section of a branch proved to be a biologically, statistically, and practically more feasible sampling unit. For a relative estimate of overwintering populations of WALH eggs, this sample unit provides a precise density estimate. Also, when these



Figure 33.--Distribution of proportion for summer eggs of <u>T. pomaria</u> in different sampling sites in Wasem orchard, 1977. Letters U, D, N, S, W, E stand, respectively, for upper, lower, north, south, west, and east of the trees. Numbers refer to numbers given to trees.

populations are small, it provides a large area of sampled habitat. While more accurate estimates of population would be necessary for detailed population-dynamics studies, subsampling of a portion of this original sample could be expanded to meet a higher precision requirement (< 10% SE of mean).

Overwintering eggs of the WALH were aggregated in experimental apple orchards and their theoretical distribution did not differ significantly from the negative binomial. ANOVA comparisons suggested the main source of variance within the orchard was intertree variation. It was concluded that density differences on mixed varieties of apple trees accounted for this source of variation. In more disturbed orchards there was significant variation between levels of trees. This probably was a result of higher WALH population in the upper part of the trees in response to more vigorous shoot growth and pruning practices. Only in one of the orchards were significant differences found between quadrants and two-way interactions. This commercial orchard received regular pruning practices and pesticide application. These management practices probably contributed to these higher variations. Similar sources of variations as observed for the WALH overwintering eggs were found for parasitised eggs by An.epos. However, the significance of F was smaller for <u>An.epos</u> in comparison to source of variation for total WALH egg counts. The distribution of parasitised eggs closely follows the distribution of the WALH in relation to intertree and between-tree differences.

In future sampling designs, between-tree variation in WALH and parasitised eggs of the WALH may be reduced by increasing the number of trees sampled/orchard. Due to different varietal, environmental, and management conditions, however, some residual variation will persist and further increases in sample size will not eliminate these variations. In orchards with different growth patterns or where different pruning practices are used, stratified samples of leafhoppers and parasites should be taken to account for this pattern of plant growth (e.g., upper, lower, directional). (See Tables 29-34.) Also, differential pesticide-induced mortalities to either WALH or <u>An.epos</u> can greatly alter their distribution. These factors and other similar management manipulations may necessitate larger sample size or other stratified sampling schemes.

Graphical interpretation and regression analysis of total overwintering WALH eggs and WALH eggs parasitised by <u>An. epos</u> suggest that parasitised eggs coincide with the distribution of the WALH. Also, parasitism increases with increased aggregation and densities of the host. A positive response to the aggregation of its host is an important component of numerical and functional response of a parasitoid (Griffith & Holling, 1969). It also is reflective of a density-dependent relationship. Distributional coincidence relates to host specificity and host finding. It is an important attribute of an effective biological control agent (Doult, 1959).

In this study, the spatial coincidence of <u>An</u>. <u>epos</u> with overwintering eggs of the WALH suggests a high level of adaptation between

two species. Considering the parasitoid is well synchronized to availability of the WALH overwintering eggs (Sections II and III), protection and support of <u>An.epos</u> in this phase of interaction are highly recommended. The possibilities for carrying out such conservation were discussed in Sections II and III.

# SECTION V

# SUMMARY FOR MANAGEMENT RECOMMENDATIONS AND FUTURE RESEARCH

# Introduction

In the previous sections, management strategies for the WALH were discussed in some detail. In this section these strategies are integrated and summarized systematically from the start to the end of the growing season. Also, the potential for additional management tactics and future research needs for evaluating these practices are discussed. Because of the importance of environmental monitoring and the incorporation of this information into predictive models in Michigan apple pest management (Croft et al., 1976; Welch et al., 1978), the orientation of the present research has been toward this approach.

# Management of the WALH in the First Generation

A phenological model based on a degree day scale has been developed (Figures 20 and 21) which mimics seasonal development and activity of the WALH. Also included is range of activity for <u>An</u>. <u>epos</u> and <u>Ap</u>. <u>typhlocyba</u> relative to thermal threshold and degree day summation for the WALH. Although the model needs further validation and refinement, at present it provides pest managers with a tool for approximating and predicting the sampling times for biological events

related to WALH management. It also enables one to avoid excessively frequent samplings, which are time consuming. According to this model, nymphal emergence from the overwintering eggs can be predicted in advance and recommendations made to maximize the effect of pesticides on the WALH and minimize their effect on <u>An</u>. <u>epos</u> and Ap. typhlocyba.

To synchronize the model early in the season, the appearance of red eyes on the developing embryo is recommended as a biological reference point. When the first red eyes appear on the developing embryo, percentage egg development should be sampled and estimated from the relationship described in Section II. Equivalent degree days for percentage development can then be calculated from the regression lines presented in Section III, and the percentage egg hatch similarly predicted. According to this model, spray application should be delayed somewhat until hatch is completed. This should subject more female nymphs to pesticides, while minimizing pesticide effects on the first pulse of An. epos emerging from overwintering eggs. Also, it allows a partial population of Ap. typhlocyba associated with early nymphs to be less subjected to spray effect. These early nymph populations escaping spray effects are males, which will not pose a direct threat to the next generation. However, if this early nymphal population is large enough in number to cause damage, pesticides should be applied sooner. Further consideration is necessary and further research is needed to improve these management strategies; these will be discussed from here on.

I. Development of a sampling method for estimation of overwintering WALH populations is needed. Precise estimation of these populations can be used to estimate accurately the percentage eggs developed to the red eye stage. Also, it can be used to estimate the potential pest population density in the first generation. Raw data collected on the distribution of overwintering eggs of the WALH and analyzed in relation to the coincidence of the parasite and its host (Section IV) are presented in Appendix B. These data may be useful in developing a more precise sampling scheme for overwintering eggs in the future.

Because the major source of variation in this study was intertree variation, additional and enlarged distributional studies on overwintering eggs of the WALH from more homogeneous and heterogeneous tree populations are recommended. Homogeneous samplings would provide data on the basic components of population aggregation, whereas heterogeneous sampling might provide a generalized sampling scheme for orchards of mixed varieties. Also sampling designs used in this study may be precise for estimating relative emergence and activity of nymphs, it probably is not enough for absolute population density estimates and detailed population dynamics studies. Such absolute density estimates, without considering the growth feature of the apple trees, will be relatively imprecise. Long-term research is needed to incorporate variable tree growth features into population estimates.

II. Three mortality factors, parasitism, egg degeneration, and nymphal dispersal, have been shown to decrease the impact of the overwintering population of the WALH in the spring generation. The

magnitude of these mortalities is usually so large that it prevented the WALH from being economically important in the first generation. These mortalities also may have affected the slope of developmental curves presented in Section III. The influence of these factors should be investigated in the future, while considering the following points:

1. The egg parasitoid <u>An</u>.epos is well adapted temporally to the overwintering eggs of the WALH (Section II) and spatially it has a positive response to aggregation of its host (Section IV). It is not known, however, how many generations of parasitoid occur normally. The minimum thermal threshold for development of overwintering eggs is estimated at  $48^{\circ}$  F in this study. Estimated base temperature for development of An.epos has been estimated at 46.12° F (Gutierrez<sup>1</sup>: personal communication with Brian A.  $Croft^2$ ). Also, An. epos does not have any overwintering diapause in California (Doutt & Nakata, 1973). These factors may allow parasitoids to be more active on the WALH overwintering population early in the fall during the oviposition period of the WALH, and early in the season before and during the period in which overwintering eggs are developing and hatching. Therefore, this phase of interaction of An.epos and its host should be precisely investigated. Three pulses of parasitoid emerge from the overwintering eggs occur: (a) early in the spring, (b) early in the summer, and (c) late in the summer. This specific emergence pattern originates

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from late summer to early spring interactions of T. pomaria and An. epos. McKenzie and Beirne (1972) observed only two pulses of parasitoid emergence: (a) early in the growing season and (b) early in the summer. They concluded that overwintering parasitoid population in an advanced phase of development gives rise to An.epos adults early in the growing season and those in later developmental stages emerge as adults early in the summer. We hypothesized that possibly the first pulse of parasitoid that emerges early in the spring can further parasitise overwintering eggs, and this gives rise to the third pulse of An. epos adults late in the summer. Another hypothesis is that parasitisation of overwintering eggs of the T. pomaria by An.epos originating from different alternative hosts and synchronization of emergence pattern to the availability of these alternative hosts accounts for these observations. In either of these two hypotheses, the delay in parasitoid development can not be completely accounted for. <u>An</u>.epos can complete a life cycle in 16-21 days during spring and summer in California (Doutt & Nakata, 1973) and in 2-3 weeks in British Columbia (McKenzie & Beirne, 1972) on grape leafhopper. Therefore, it is possible that certain physiological events induce a summer diapause in immature stages of An.epos in overwintering eggs of the WALH. This needs to be investigated further.

2. A high percentage of overwintering WALH eggs was degenerated in this study. The magnitude of this mortality was best correiated to the rise and fall of temperature and rapid plant growth during development of overwintering eggs (Section II). The influence of these factors should also be investigated further and incorporated in future predictive models.

3. While nymphs are dispersing from the overwintering site to the underside of leaves, high mortality could be expected; this to be studied in future research.

III. Research is necessary to establish a precise economic threshold value for the WALH and justify the necessity of chemical control.

IV. Empirically, it is believed the younger the nymphs, the more susceptible they are to pesticides. The oldest nymphal stages susceptible to pesticides should be determined to justify a delay in spraying programs without economic loss.

V. Different life stages of <u>Ap. typhlocyba</u> are subjected to pesticides throughout the season. Partial population of this parasitoid can be protected by properly timed spray programs, as discussed earlier. Management strategies are necessary to conserve this parasitoid further. Nothing is known about the effect of pesticides on this parasitoid. Since in some chemically sprayed orchards this parasitoid is common, it is anticipated that study of the effect of insecticides on this parasitoid in terms of selectivity might be fruitful. Further support for this parasitoid can be achieved by ground cover management. This parasitoid makes its cocoon in the soil, under the canopy and more toward the interior of the tree. Research is necessary to determine the distribution of these cocoons in the ground cover under the canopy. This can be achieved by direct counting of cocoons, or monitoring of emergence of <u>Ap. typhlocyba</u>

adults from the soil, or by sampling mummified parasitised leafhoppers on the trees.

#### Management of the WALH in the Second Generation

Leafhoppers that escape natural or chemical control programs in the first generation lay eggs in the leaves and could be a threat to foliage in the second generation. Management of such populations can be achieved in several ways. Research is necessary to estimate the potential pest population density far in advance. An absolute density estimate of the adult population can be obtained from the last instar exuvia which remains on the apple leaves during the growing season. Effects of severe weather conditions on exuvia loss, estimates of sex ratio, percentage parasitised adults by Ap. typhlocyba, and fertility of females are needed to better predict potential pest population for the next generation. If an economic threshold value were also available for this pest, proper recommendations could be better made for spray programs since predicted egg density could be assumed to reflect second generation potential pest population. This assumption is plausible because the effect of An.epos on summer eggs is small and Ap. typhlocyba causes mortality only to adult WALHs. If future research proves a higher efficiency of An.epos on summer WALH eggs or if a differential feeding behavior of parasitised and nonparasitised nymphs occurs, then these factors also should be considered in forecasting estimates of potential pest injury.

If the potential pest population is large in the second generation and chemical control is necessary, nymphal emergence can

be predicted from the developed model (Section III). The first egg that develops to the red eye stage or the first nymph to emerge should be used as a reference point for synchronization of the model. In addition to previously mentioned nymphal density estimates, two other alternatives could be used for the same purpose. The first alternative is to sample nymphs and summer eggs when a small portion of nymphs has emerged and the activity of females has almost ended (Figure 21). This requires a precise sampling procedure for nymphs and eggs. The other alternative is more precise estimation of nymphs in the early emergence period and estimation of the second generation egg hatch (Figure 21). This requires a fully validated model applicable to different environmental conditions.

Similar to the first generation, a delay in spray application is recommended. This delay in spraying would increase the survival of <u>Ap. typhlocyba</u>. It also would allow partial female nymphal population to develop to the adult stage and provide host eggs for the third pulse of <u>An. epos</u> emerging from overwintering eggs. To achieve a better management program, the susceptibility of the older nymphal WALH stages to pesticides and the economic threshold of this generation should also be investigated.

#### Management of the Overwintering Population of the WALH

A third pulse of <u>An</u>. <u>epos</u> emerges in synchrony with oviposition period of the second generation WALH in late summer. At this time of the year, the application of pesticides in apple orchards is ended. This provides the most promising biological window for the

activity and manipulation of this parasitoid. Several alternative hosts for <u>An.epos</u> are found in Michigan. We reared this egg parasitoid from grape leafhopper eggs on grape leaves in apple orchards and from overwintering eggs of <u>E. maligna</u> on apple. <u>E. maligna</u> as an alternative host of <u>An.epos</u> may be an important factor in the population dynamics of the WALH in undisturbed habitats, but practically it is not possible to use this species as an alternate host in commercial apple orchards (see Appendix A). The grape leafhopper is more promising for management purposes. Emergence of the <u>An.epos</u> from the observed grape leafhopper eggs, synchronized well with the oviposition period of the second generation WALH. Therefore, it is hypothesized that <u>An.epos</u> is dispersing between these two hosts. Research is necessary to test this hypothesis. If such dispersal is occurring, manipulation of the parasitoid should be feasible on patches of wild grape in apple orchards or in orchards near vineyards.

Finally, from a management standpoint, since the WALH is a pesticide-induced pest in commercial apple orchards, it is expected that the reduction in pesticides used in apple orchards will reduce the intensity of the WALH problem. However, pesticides will probably remain as part of apple pest management programs for a long time to come and, therefore, recommended management strategies for other apple pests should be coordinated with management tactics for the WALH.

Recommendations made herein are based on life history studies of the WALH and its natural enemies. The natural mortality factors having the greatest influence on population dynamics of the WALH

appear to be those influencing the survival of the overwintering population. However, the overall role of these factors in regulation of the WALH population can not be overemphasized. Detailed population dynamics studies are necessary to determine key factors contributing to regulation of this insect and to improving management strategies. This research can be best achieved by studying the population dynamics of the WALH in a heavily infested apple orchard, unsprayed for several sequential seasons. LITERATURE CITED

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APPENDICES

APPENDIX A

BIONOMICS OF FOUR SPECIES OF APPLE LEAFHOPPER IN MICHIGAN

### APPENDIX A

# BIONOMICS OF FOUR SPECIES OF APPLE LEAFHOPPER IN MICHIGAN

# Introduction

In addition to the WALH, there are several damaging species of leafhopper which occasionally occur in commercial apple orchards and often are found in abandoned orchards (Sections I and II). They include the species <u>Empoasca maligna</u> Walsh (green apple leafhopper), <u>Empoasca fabae</u> (Harris) (potato leafhopper), and <u>Erythroneura</u> <u>lawsoniana</u> Baker (oblique-striped apple leafhopper). During the course of this study on the temporal and spatial distribution of the WALH and its natural enemies, research was also conducted on these associated leafhoppers for several reasons: (1) More information on their bionomics was necessary to avoid errors relative to the bionomics of the WALH. (2) It was expected the life system of the WALH was linked to these associated leafhoppers by interspecific competition and the same natural enemies. (3) Researchers working on funded projects for common pest species should contribute to the knowledge of other less economic species.

This study contributes knowledge to this group of leafhoppers since no similar studies have been done in Michigan. Also, some of the findings reported herein are new for these species and the leafhopper complex. Detailed studies on morphology and biology of these species can be found in Ackerman and Isely (1931). Also, Metcalf (1968) gave references to most publications about each and further

references can be found in Delong (1971). Methods and materials used in this study were the same as described for sampling of the WALH in egg and adult stage (Sections II and IV).

# E. maligna

In orchards 1 and 2, 1976, the distribution of overwintering eggs of this species was determined on every 15 cm interval of a 75 cm or longer apical section of a branch, as described for the WALH (Section IV). Results of this study are presented in Table 35. Considering egg density and surface area on each section sampled, it was concluded that E. maligna egg densities changed in a descending order from the apical part of the branch to the base of the branch for orchard 1. In spite of larger sample size taken in orchard 2, results for this same analysis were more variable, probably because of lower densities and the more heterogeneous branch characteristic of this orchard (Section II, description of study orchards). Comparing these results with Table 27 and Figure 24 (Section IV) for the WALH, it can be concluded that the preferences of these two species for overwintering oviposition sites differ somewhat but there is still considerable overlap in their preferred oviposition sites.

In orchard 1, 1976, development of these eggs to red eye developmental phase started on April 30 and by June 4 egg hatch was completed (Figure 35). In orchard 2, 1976 initiation of egg development to the red eye phase was not determined but egg hatch was completed on May 21. Comparing these results with Tables 1 and 2

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		Distance	e From Apical	of Branch (	(in cm)	
	0-15	15-30	30-45	45-60	60-75	75-90
Orchard 1						
Sample size	60	60	60	60	60	44
Mean ± standard error	<b>1.32±0.3</b> ]	1.13±0.27	<b>1.20±0.27</b>	1.23±0.33	1.15±0.29	0 <b>.9</b> 7±0.28
Orchard 2						
Sample size	80	80	80	80	80	L L
Mean ± standard error	0.14±0.04	0.09±0.04	0.21±0.05	0.40±0.07	<b>0.21±0.05</b>	<b>0.41±0.8</b> 0

(Section II) for the WALH, development and hatch of overwintering eggs of <u>E</u>. <u>maligna</u> is about 1 week later than the same events for the WALH. First new eggs of <u>E</u>. <u>maligna</u> were observed on July 24 and July 10, respectively, in orchards 1 and 2 in 1976. Results for the seasonal distribution of adult <u>E</u>. <u>maligna</u> in different orchards and in different years are presented in Tables 36-38 and Figures 34-35. Comparing these overall results with seasonal distribution of <u>I</u>. <u>pomaria</u> (Section II), we concluded there is broad overlap in the seasonal distribution of these two species. However, <u>E</u>. <u>maligna</u> probably is slightly behind in its seasonal activity from the first generation <u>T</u>. <u>pomaria</u>.

Date	Male	Female	
 6/13 6/21 6/28 7/5 7/12 7/19 7/26 8/2 8/9 8/16 8/23 8/30	0 10 218 364 156 85 72 15 14 4 1 b	0 6 157 328 332 314 243 157 83 36 3 5 b	
9//	0	0	

Table 36.--Total number of adult <u>E</u>. <u>maligna</u><sup>a</sup> captured on 12 yellow traps in orchard 1, 1975.

<sup>a</sup>Only one individual had a cyst of unidentified parasitoid on the abdomen on 7/19 and another individual had a parasite cyst on 8/16.

<sup>b</sup>Missed information but not very common.

Date	Male	Female
6/11	0	0
6/18	27	6
6/25	686	389
7/3	1,803	845
7/10	1,098	1.844
7/17 <sup>a</sup>	602	1,400
7/24	704	1.348
8/3	261	787
8/10	91	397
8/18	19	136
8/25	1	30
9/1	Ō	2
9/9	Ō	Ō
9/16	Ō	Ō
9/23	Ō	Ĩ
-,	-	·

Table 37.--Total number of adult <u>E</u>. <u>maligna</u><sup>a</sup> captured on 12 yellow traps in orchard 1, 1976.

 $^{\rm a}{\rm Only}$  one male and one female had a cyst of an unidentified parasitoid on the abdomen on 7/17/76.

Table 38.--Total number of <u>E</u>. <u>maligna</u> captured on 6 yellow traps in orchard 2, 1976.

Date	Male	Female
6/11	0	0
6/18	2	Ō
6/25	2	6
7/2	2	4
7/10	0	12
7/17	1	5
7/24	0	2
8/3	1	0
8/11	0	1
8/18	0	0


Figure 34.--Seasonal distribution of adult E. maligna, orchard 1, 1975.





### <u>Natural Mortality Factors of E. maligna and</u> <u>Interactions of E. maligna-T. pomaria</u> <u>Life Systems</u>

In 1975, a study was in progress to develop a series of life tables for the WALH. Since the population of associated species of leafhoppers outnumbered the population of the WALH, this study was discontinued in this orchard. However, with some modifications in sampling techniques, the population changes for <u>T</u>. <u>pomaria</u> and <u>E</u>. <u>maligna</u> were estimated through time by sampling overwintering populations of both species.

In orchard 1, two study plots were selected. In each plot seven Ida Red apple trees, and on each tree full branches, were randomly sampled. Sampling time was after overwintering eggs of both species were completely hatched. The study was continued in 1975-1977. On each branch, total leaf clusters, total eggs, and total parasitised eggs of each species were counted. Characteristics of eggs of these two species and parasitised eggs of <u>T</u>. <u>pomaria</u> by <u>An</u>. <u>epos</u> are the same as described in Section II. Parasitised eggs of <u>E</u>. <u>maligna</u> are progeny of three species of parasitoids, <u>Anagrus epos</u> Girault, <sup>1</sup> <u>Anagrus armatus</u> Ashmead<sup>2</sup> from the family Mymaridae, and <u>paracentrobia sp<sup>3</sup></u> from the family Trichogrammatidae.

<sup>&</sup>lt;sup>1</sup>Identified by G. Gordh, Department of Entomology, University of California/Riverside, Riverside, California.

<sup>&</sup>lt;sup>2</sup>Identified by E. E. Grissell, Insect Identification and Beneficial Introduction Institute, Agricultural Research Center, West Administration Building, Beltsville, MD 20705.

<sup>&</sup>lt;sup>3</sup>Identified by E. E. Grissell.

No attempt has been made to differentiate between developmental stages of these three species of parasitoid on <u>E</u>. <u>maligna</u>, but the cumulative effect of these parasitoids on the host were determined by counting larvae, pupa, and emergence holes of parasitoids. Pooled results for each leafhopper species in each plot and for different years are presented in Table 39. These data are weighted for 325 leaf clusters (minimum leaf clusters counted per plot per year) and are presented in Table 40.

These data suggest that the populations of <u>E</u>. <u>maligna</u> were continuously increasing in both plots, but the rate of increase was much faster in plot 1, and in either case the density response of parasitoids to this population change was very slight. This slow response of the parasitoids suggests they were not a significant control factor for the three-generation <u>E</u>. <u>maligna</u> population. Comparison of population density of <u>E</u>. <u>maligna</u> between the two plots through time suggests that <u>E</u>. <u>maligna</u> has a very slow rate of dispersal. This behavior was also observed in trap catch data and often observations taken in this orchard. In 1975 a population of <u>E</u>. <u>maligna</u> adults was observed in a hot spot in orchard 1. Over a 3-year period their foci only increased to the periphery of the original infestation site.

Population counts for <u>T</u>. <u>pomaria</u> suggested that overwintering population increased in plot 2 but levels were rather constant in plot 1. In both plots the response of <u>An</u>. <u>epos</u> to the WALH was more rapid than in response to <u>E</u>. <u>maligna</u>. Overall population of

			Mean ±		1. Po	naria			E. mal	igna	
weby	ptord	Total Losf	Standard	Tota	il Eggs	Total	Parasitised	Tota	1 Eggs	Total P	arasitised
		Cluster <sup>b</sup>	for Leaf Clusters	Total	Mean ± Standard Error	Total	Mean ± Standard Error	Total	Mean ± Standard Error	Total	Mean ± Standard Error
1975	L	325	23.21±2.0 <b>4</b>	31	2.21±0.47	ω	0.57±0.17	96	6.86±2.48	19	1.36±0.53
1975	2	349	24.93±2.13	11	1.21±0.38	ъ	0.36±0.23	13	<b>0.93±0.29</b>	2	0.14 <u>±</u> 0.10
1976	-	490	35.00±3.20	58	4.14±1.30	19	1.36±0.80	394	<b>28.14± 8.9</b> 7	30	2.14±0.61
1976	7	445	31.79±2.25	36	2.57±0.48	e	0.21±0.11	18	<b>1.29± 0.54</b>	0	0.00
1977	-	467	33.36±3.26	42	3.00±1.03	15	1.07±0.71	849	60.64±11.20	41	2.93±0.92
1977	5	498	35.57±2.77	99	4.71±0.97	15	1.07±0.43	28	2.00± 0.46	0	0.00
	a								<u> </u>	.	

Table 39.--Change in population density of overwintering eggs of  $\underline{I}$ . pomaria and  $\underline{E}$ . maligna in two apple plots in orchard 1, through 3 continuous years.

<sup>a</sup>Where other conditions for two plots were assumed to be equal, plot <u>2</u> received an application of fertilizer and an application of fungicide at the very beginning of the study period.

<sup>b</sup>In each plot seven Ida Red apple trees were randomly selected and tagged. Every year two branches from each tree were selected randomly.

⁄ear in each plot.	aligna	Total Eggs Parasitised	19.00	1.86	19.90	0.00	25.53	0.00
usters for each y	EI 	Total Eggs	96.00	12.11	261.33	13.15	590.85	18.27
ited for 325 leaf cl	maria	Total Eggs Parasitised	8.00	4.66	12.60	2.19	10.44	9.79
of Table 39 weigh	T. po	Total Eggs	31.00	15.83	38.47	26.29	29.23	43.07
Total counts (		Plot	l	8	-	N	-	7
Table 40.		Year	1975	1975	1976	1976	1977	1977

<u>E. maligna</u> increased faster than <u>T. pomaria</u> over the 3-year period.

Generally speaking, many factors may affect the population dynamics of <u>E</u>. <u>maligna</u> and prevent it from rapidly becoming a serious pest over an extended area. These factors were not studied in detail. However, its monovoltine life cycle, low rate of dispersal, and partial effects of parasitoids seem to be important biotic factors influencing the abundance of this species. These factors alone, however, were not enough to regulate <u>E</u>. <u>maligna</u> population. Observations in other abandoned orchards, off-sprayed for many years, showed this species to be the most common leafhopper in such orchards.

<u>An. epos</u>, <u>Ap. typhlocyba</u>, late season mortality of adults by cold temperature, and growth characteristics of the plant were previously mentioned as important factors influencing the population dynamics of <u>T</u>. <u>pomaria</u> (Sections I-V). Where <u>E</u>. <u>maligna</u> and <u>T</u>. <u>pomaria</u> occur together in the same habitat and in undisturbed conditions, their life systems interact appreciably. Some influence of <u>E</u>. <u>maligna</u> on the <u>T</u>. <u>pomaria</u> life system may be related to the former serving as an alternative host for <u>An. epos</u>. Its competition with the WALH for overwintering oviposition site and food at high densities are almost certainly important factors. These influences could be important in explaining the population dynamics of the WALH over a long period of time in an endemic system. However, these features probably have little impact in commercial apple orchards, and therefore show little promise for use in IPM of the WALH.

#### E. fabae

Each spring the potato leafhoppers migrate from the southern United States northward into Michigan and Canada via the prevailing winds (Delong, 1971). The serious injury of this insect in Michigan apple orchards has been observed on young apple plantations and on suckers and terminals of more mature trees. The seasonal distribution of adults of this species in orchard 1 in 1975 and 1976 was recorded and is presented in Tables 41 and 42 and Figure 36. Data suggest that the potato leafhopper was most commonly found early in the growing season in apple orchards.

Table 41.--Total number of adult  $\underline{E}$ . <u>fabae</u> captured on 12 yellow traps in orchard 1, 1975.

Date	Male	Female	
5/23	0	36	
5/30	5	150	
0/0	4	114	
6/13	2	39	
6/21	40	66	
6/28	15	54	
7/5	74	94	
7/12	73	77	
7/19	36	38	
7/26	17	23	
8/2	15	4	
8/9	4	5	
8/16	1	5	
8/23	11	5	
8/30	a	a	
9/7	14	14	
9/14	2	6	
9/21	ī	2	
9/28	1	ī	
10/5	j	Ì	
10/12	Ó	ò	
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<sup>a</sup>Missed information but not very common.





Date	Male	Female	
5/28 6/4 6/11 6/18 6/25 7/3 7/10 7/17 7/24 8/3 8/10 8/18 8/25 9/1 9/9	7 4 1 2 0 0 0 1 5 1 1 0 1 0	0 5 2 8 26 1 2 0 0 0 1 1 1 0 0 0 0 0 0 0 0	

Table 42.--Total number of adult  $\underline{E}$ . <u>fabae</u> captured on 12 yellow traps in orchard 1, 1976.

Occasionally damage of this insect can be high in young apple plantations. The extent of this insect as a pest in Michigan apple orchards probably depends greatly on its density and time of migratory arrival. This leafhopper is the second important leafhopper pest in Michigan commercial apple orchards. It should be considered more in future IPM programs in apple orchards.

## E. lawsoniana

This species is a more southernly adapted leafhopper in the United States (Ackerman & Isely, 1931), but it is also common in abandoned orchards in Michigan. Data on the seasonal distribution of adults for this species, recorded during 1975-1976, are presented in Tables 43-45 and Figures 37-39. Some individual adults of this

Date	Male	Parasitised Male	Female	Parasitised Female	Male + Female
5/23				••	2 <sup>C</sup>
5/30					0
6/6					0
6/13					0
6/21					2 <sup>C</sup>
6/28					2 <sup>C</sup>
7/5					13 <sup>C</sup>
7/12					8 <sup>C</sup>
7/19	15	0	8	0	23
7/26	23	2	12	2	35
8/2	38	8	21	2	59
8/9	16	6	22	5	38
8/16	8	1	9	1	17
8/23	1	0	2	0	3
8/30	b	b	b	b	5 <sup>b</sup>
9/7	11	1	5	1	16
9/14	12	0	14	0	26
9/21	8	0	5	0	13
9/28	5	0	7	0	12
10/5	16	0	18	0	34
10/12	22	5	15	4	37
10/19	24	5	23	3	47

Table 43.--Total number of adult <u>E</u>. <u>lawsoniana</u> and total parasitised<sup>a</sup> adult <u>E</u>. <u>lawsoniana</u> captured on 12 yellow traps in orchard 1, 1975.

<sup>a</sup>Parasitised leafhoppers have cyst on abdomens.

<sup>b</sup>Not identified for sex and parasitism.

<sup>C</sup>Not identified for sex.





Date	Male	Parasitised Male	Female	Parasitised Female
5/28	55	0	9	0
6/4	27	0	11	0
6/11	36	0	16	0
6/18	15	0	11	0
6/25	17	0	5	0
7/3	15	0	4	0
7/10	7	0	10	0
7/17	17	0	9	0
7/24	21	1	13	0
8/3	71	2	29	3
8/10	40	7	16	3
8/18	23	5	15	2
8/25	14	3	11	2
9/1	14	1	6	3
9/9	5	0	15	0
9/16	9	1	19	2
9/23	19	0	24	0
9/30	15	1	12	2
10/7	11	2	9	2
10/14	8	1	4	1
10/21	0	0	0	0

Table 44.--Total number of adult <u>E</u>. <u>lawsoniana</u> and total parasitised adult <u>E</u>. <u>lawsoniana</u> captured on 12 yellow traps in orchard 1, 1976.



Figure 38.--Seasonal distribution of adult <u>E. lawsoniana</u>, orchard 1, 1976. Numbers refer to those parasitised by an unknown parasitoid.

Date	Male	Parasitised Male	Female	Parasitised Female
5/28	105	0	28	0
6/4	32	0	8	0
6/11	36	0	20	0
6/18	9	0	10	0
6/25	20	0	8	0
7/2	6	0	9	0
7/10	15	0	16	0
7/17	13	0	17	1
7/24	201	2	44	0
8/3	149	0	38	0
8/11	31	0	15	0
8/18	7	0	6	0
8/25	3	0	6	0
9/1	8	1	5	0
9/9	10	0	15	0
9/16	28	0	20	0
9/23	30	0	29	0
9/30	53	0	54	0
10/7	37	0	34	0
10/14	44	0	56	1
10/21	5	0	9	0

Table 45.--Total number of adult <u>E</u>. <u>lawsoniana</u> and total parasitised adult <u>E</u>. <u>lawsoniana</u> captured on 6 yellow traps in orchard 2, 1976.



species carried a cyst on their abdomens that contained a parasitoid larva. This parasitoid was not reared to adult, but the observed cyst is similar to parasitic symptoms produced by dryinid parasitoids on leafhoppers, in general.

## APPENDIX B

# RAW DATA ON SPATIAL DISTRIBUTION OF OVERWINTERING AND SUMMER EGGS OF THE WALH

.

Sample Stat										Tree	Numbe	er.							
Number Stat			-			2			e			4			5			9	
	sn									Str	atum								
		đ	Down Out	Down In	đ	Down Out	Down In	а Л	Down Out	Down In	đ	Down Out	Down In	Ъ.	Down Out	Down	ď	Down Out	lown In
Total	sõõa	13	8	9	0	e	m	-	-	e	و	4	e	2	0	2	9	e	0
Parasi	tised	2	0	4	0	2	m	-	0	m	4	2	2	S	0	2	-	2	0
, Total	s66a	4	2	m	ъ	e	5	9	2	e	•	۳	4	23	-	-	4	2	2
2 Parasi	tised	~	0	~	m	0	-	~	-	0	0	-	-	80	0	0	0	0	4
Total	s66a	~	-	m	~	0	ى س	•	0	2	12	7	-	0	4	0	2	0	0
o Parast	tised	-	0	0	8	0	ñ	0	0	0	6	m	-	•	-	0	•	0	0
Total	s66a	2	-	-	-	2	0	12	-	4	ñ	S	٢	10	0	0	Ś	4	0
4 Parast	tised	0	-	0	0	0	0	2	-	0	2	2	ε	S	0	0	-	0	•

## APPENDIX B

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-		Tree Number			_			 C	7	
-		Quadrant	North	West	South	East	North	West	South	East
		Sample Number	B	B A	B A	BA	A B	B A	BA	<b>A</b> 8
		Total Eggs	0 2	٥٣	с С	04	00	00	~-	00
	Down	Degenerated	0-	0 N	0 -	00	00	00	00	00
		Parasi- tised	00	00	00	0-	00	00	00	00
		Total Eggs	3	C CI	00	- 2	NO	40	5 ]	-0
	đ	Degenerated	0-	00	00	0-	NO	40	0-	00
		Parasi- tised	00	00	00	0-	00	00	00	00

				Down			٩Ŋ	
Tree Number	Quadrant	Sample Number	Total Eggs	Degenerated	Parasi- tised	Total Eggs	Degenerated	Parasi- tised
	North	B A	-0	00	<b>1</b> 0		-0	00
ſ	West	8 A	00	00	00	0	00	00
n	South	<b>A</b> 8	00	00	00	00	00	00
	East	A 8	-0	00	00	0-	00	0-
	North	8 Y		-0	00	- 4		0-
•	West	<b>A</b> 8	00	00	00		00	00
4	South	8 A	50	00	0 7	0-	00	00
	East	B A	-0	00	00	-0	00	00

Table 47.--Continued.

	Parasi- tised	-0	~ ~	0-	00	0-	00	00	-0
Чр	Degenerated	00	2	0 -	00	00	00	00	00
	Total Eggs	0	4 0	ς 4	-0	0-	-0	-0	- 15
	Parasi- tised	00	-0	00	0-	00	0 0	40	00
Down	Degenerated	0-	0-	0-	-0	00	00	0 -	0
	Total Eggs		~~~	-17			- 6	9 -	04
	sample Number	A B	<b>A 8</b>	8 A	B A	B A	B A	B A	BA
	Quadrant	North	West	South	East	North	West	South	East
ł	l ree Number		u	ი			,	٥	

Table 47.--Continued.

	Troo	Number		-	-			c	V		
its mortali sampled.		Quadrant	North	West	South	East	North	West	South	East	
ity factors,	Samulo	Number	A B	<b>A</b> 8	<b>A</b> 8	<b>A</b> 8	<b>A</b> 8	<b>A</b> 80	8 A	A 8	_
orchard 2		Total Eggs	00	00	0-	00	00	-0	0-	0 0	
., 1976. Each	Down	Degenerated	00	00	00	00	00	00	00	-0	
count is to		Parasi- tised	00	00	00	00	80	00	00	00	
tal for 5(		Total Eggs	30	- 2	50	00	0-	00	<u>ں ح</u>	00	
) cm² of a brar	đ	Degenerated	00	0-	00	00	00	00	0-	00	
Jch		Parasi- tised	0 0	00	0-	00	00	00	40	00	

Table 48.--Raw data on inter- and intratree distribution of overwintering eggs of T. pomaria and

ŀ		-13		Down			dŊ	
Number	Quadrant	vamp i e Number	Total Eggs	Degenerated	Parasi- tised	Total Eggs	Degenerated	Parasi- tised
	North	B A	0	0-	00		-0	00
ç	West	<b>A</b> 8	90	7	0-	06	0 0	60
n	South	B A	0-	00	00	0 7	0-	0-
	East	B A	00	00	00		00	
	North	8 8	o 22	-0	00	νΩ	-0	~ ~ ~
•	West	B A	0 m	00	50	53	0 0	тo
4	South	8 A	O IS	0 0	0-	ωω	00	00
	East	BA	00	00	00	0 M	0 -	0-

Table 48.--Continued.

T 500		Camplo		Down			Up	
Number	Quadrant	Number	Total Eggs	Degenerated	Parasi- tised	Total Eggs	Degenerated	Parasi- tised
	North	¥ 8	00	00	00	20	00	00
Ĺ	West	A 8	00	00	00	00	00	00
n	South	<b>4</b> 8	00	00	00	00	00	00
	East	<b>A</b> 80	00	00	00	-0	00	00
	North	₹ 83	0-	00	00	0 0	-0	00
,	West	<b>A</b> 8	0-	00	00		0-	00
٥	South	<b>A</b> 8		-0	00	0-	00	00
	East	<b>A</b> 8	00	00	00	-0	-0	00

Table 48.--Continued.

rwintering eggs of <u>T</u> . <u>pomaria</u> and is total for 50 cm <sup>2</sup> of a branch
of ove count
listribution ( 1976. Each (
intratree c orchard 3,
nter- and factors,
ta on i tality 1.
Raw dai its mou samplec
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		Camalo		Down			đ	
l ree Number	Quadrant	Number	Total Eggs	Degenerated	Parasi- tised	Total Eggs	Degenerated	Parasi- tised
	North	A B	4	0-	40	4	0 2	4 L
-	West	B A	00	0	90	11 4	L 4	90
_	South	8 A	14 8	δ	10 4	21 9	-0	15 3
	East	BA	10	- 2	0-	6[	4 8	мО
	North	A 8	- ~	- ~	00	0 7	-0	00
c	West	<b>A</b> 8	00	00	00	7 ]	0 -	00
V	South	8 A	0 0	0-	00	0-	00	00
	East	B A	-0	-0	00		00	0-

		Comes		Down			Чр	
Number	Quadrant	Number	Total Eggs	Degenerated	Parasi- tised	Total Eggs	Degenerated	Parasi- tised
	North	BA	4	ω –	00	3	0 -	00
c	West	B A		00	0-	00	00	00
ΰ	South	<b>A</b> 8	- v	<b>ب</b> س	00	55	-0	00
	East	B A	0 00	00	0-	00	00	00
	North	B A	4 00	- m	00	~-	00	00
•	West	<b>A</b> 8	0-	0-	00	14 5	- 7	00
4	South	8 A	<del>ر</del> ا	0-	00	9 15	ოო	0 m
	East	BA	0[	0 2	60	លល	0 2	-0

Table 49.--Continued.

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Twoo		Camalo		Down			Чр	
Number	Quadrant	Number	Total Eggs	Degenerated	Parasi- tised	Total Eggs	Degenerated	Parasi- tised
	North	8 ¥	0 2	0-	00	7 5	0 -	90
Ľ	West	8 A	0-	00	00	52	00	00
n	South	8 A	ი ო	52	0-	<b>4</b> 3 7	11	00
	East	A 8	12	3 -	20	იი	2	8 0
	North	8 A	2		00	00	0 0	0-
ų	West	B A	~ ∞	- 2	6 0	55 20	22 5	61 11
D	South	<b>A</b> 8	0 m	0-	00	►4	ი 4	00
	East	8 8	02	00	00	14 8	ωω	80

					T	ree N	umber					
Quadrant	1		2		3		4		5		6	
	Down	Up	Down	Up	Down	Lev Up	el Down	Up	Down	Up	Down	Up
North	7 10 5 5 9 4 6 2 0 0	17 6 1 5 2 6 1 7 1 2	0 0 2 1 0 2 1 2 0 0	0 0 0 2 1 1 0 3 1	0 0 1 0 0 1 0 0 0	0 4 2 6 0 1 0 2 4 1	2 2 11 0 5 4 2 1 1	1 6 4 1 5 3 0 0 0	0 2 0 0 2 7 0 1 0	0 1 0 6 2 0 1 6 13	1 0 1 0 0 0 0 0 0	
West	3 3 9 6 14 1 3 0 0 3	8 2 0 4 1 2 5 4 0 1	0 0 3 1 0 0 0 0	1 0 1 0 4 3 2 0	2 5 3 4 4 1 0 5	0 6 2 1 1 2 1 4 0 1	0 4 5 14 0 2 0 5 7 0	0 0 4 1 2 5 5 3 7 1	1 4 0 0 1 5 3 2 1	0 1 0 5 1 1 0 3	0 0 1 0 4 0 0 0 0 1 0	
South	8 10 4 12 1 11 5 2 0	6 10 3 2 12 3 2 6 0	0 0 0 0 0 2 2 1 0	0 1 0 1 0 2 3 2 0	0 1 7 0 0 0 0 3 0 0	2 0 1 3 0 0 3 0 0 0	0 0 2 1 2 5 0 4 3	7 3 5 6 1 0 8 0 1 0	6 0 1 3 1 3 1 0 0	3 1 0 5 1 1 0 2	1 2 2 2 3 0 0 2	
East	4 0 7 2 0 1 3 5 2 7	1 5 0 1 6 4 4 1 1 0	1 0 0 0 0 0 0 0 0	0 1 0 0 0 0 0 0 0 0 3	1 3 0 2 3 1 0 5 0	1 0 1 0 0 0 1 1 0	1 8 3 0 0 2 18 13 4	1 1 2 3 1 1 0 2 0	2 2 0 7 0 0 0 0 0 1 0	0 1 0 0 1 0 2 0 2	0 1 0 1 2 0 3 3 0 1	

Table 50Raw data on inter- and	intratree distribution of	summer eggs of T. pomaria,
Wasem orchard, 8/13/77.	Each count is total for	one leaf (see Section IV).