

AN ABSTRACT OF THE THESIS OF

Leonard Bryan Coop for the degree of Master of Science

in Entomology presented on October 8, 1982

Title: Orange Tortrix: Parasitoid Complex and Thermal Constants

for Egg Hatch

Redacted for Privacy

Abstract approved: Glenn C. Fisher

An investigation was conducted in 1980 and 1981 on the larval parasitoid complex of the orange tortrix, Argyrotaenia citrana (Fern.), a major contaminant in cane fruits (Rubus spp.) in the Pacific Northwest. A total of 13 parasitoid species were reared from 1,350 larvae predominantly collected from red raspberries in western Oregon. The six most numerous were Apanteles aristoteliae Vier., Meteorus argyrotaenia Johan., Phytodietus vulgaris cress., Oncophanes americanus (Weed), Enytus eureka (Ash.), and Diadegma spp. The rate of parasitism averaged 20% in two commercial fields which had large larval populations of A. citrana. Conversely, five fields with relatively low density A. citrana populations averaged 66% apparent parasitism. This suggests that parasitoids may be important in maintaining orange tortrix populations at low levels. Three braconid

species, A. aristoteliae Vier., M. argyrotaeniae Johan., and O. americanus (Weed) were responsible for 82% of the difference in apparent parasitism between the two levels of infestation noted.

Each of the six most abundant species reared were studied relative to host sizes parasitized, alternate hosts in caneberries, overwintering habits, developmental rates and adult longevity at 20°C. The obliquebanded leafroller, Choristoneura rosaceana (Harris) and the omnivorous leaftier, Cnephasia longana Haw. were observed to serve as alternate hosts of M. argyrotaeniae and O. americanus but not A. aristoteliae. All three braconids plus P. vulgaris were successfully reared in the laboratory from A. citrana. Using data from constant temperature rearings and the field, A. aristoteliae was indicated to have 3-4 generations per year by a generic, computerized phenology model (PETE). Insufficient data were obtained to validate the model for predictive capabilities, however. Observations on P. vulgaris indicated that photoperiod is primarily responsible for diapause induction and termination in the laboratory.

The thermal constants 5°C and 146°C-days were derived by the lowest coefficient of variation method for the prediction of orange tortrix egg hatch. Total interval for mating, preoviposition, and 50% oviposition by adults caged over red raspberries during summer and fall averaged 3 days. Differences in adult emergence between sexes for field-collected larvae and pupae were not significant. Results on emergence, mating, oviposition, and thermal requirements for egg development are discussed relative to pest management.

Orange Tortrix: Parasitoid Complex
and Thermal Constants for Egg Hatch

by

Leonard Bryan Coop

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Completed October 8, 1982

Commencement June 1983

APPROVED:

Redacted for Privacy

Associate Professor of Entomology in charge of major

Redacted for Privacy

Head of Department of Entomology

Redacted for Privacy

Dean of Graduate School

Date thesis is presented October 8, 1982

Typed by Terrie L. Read for Leonard Bryan Coop

ACKNOWLEDGEMENTS

I would like to thank my major professor, Glenn Fisher, for his suggestions and support, both financial and moral, throughout this study.

My committee, J. Miller, R. Petersen, and E. Fichter, also provided valuable comments and advice before and during the preparation of this thesis.

Many hours were spent in the identifications of the numerous insects reared in this study. For this help I thank L. Knutson, P. Marsh, D. R. Vincent, E. E. Grissell, D. Wilder, and C. W. Sabrosky of the U.S. National Museum. Additionally, H. Townes, T. Torgersen, C. Loan, J. Miller, P. Hanson, and J. D. Lattin all helped greatly by providing their assistance and facilities in making identifications.

Special gratitude is extended to R. Lalone, G. Garth, their companies and growers for assistance in locating fields and for concern for this project.

Students who reviewed portions of this manuscript are appreciated, especially J. Furnish, B. Madar, S. Tanaka, and A. Knight.

This endeavor would not have been possible without the financial assistance provided through employment by the Department of Entomology and Professors R. Berry and B. Croft.

I express special gratitude to my family for their patience and support.

Lastly, my wife Betsy contributed unending love and wisdom throughout this experience.

TABLE OF CONTENTS

Chapter

I. INTRODUCTION.....	1
II. LITERATURE REVIEW.....	4
Taxonomy.....	4
Description of Life Stages.....	4
Distribution and History as a Pest.....	5
Biology.....	6
Parasitoids.....	8
III. PARASITOID COMPLEX.....	10
MATERIALS AND METHODS.....	10
Sample Locations.....	10
Host Collection and Rearing.....	13
Laboratory Studies.....	17
Adult Longevity.....	17
Laboratory Rearing.....	17
Developmental Periods.....	18
<u>Apanteles aristoteliae</u> ; Development at Different Temperatures.....	18
<u>Phytodietus vulgaris</u> ; Life History and Diapause Characteristics.....	19
RESULTS AND DISCUSSION.....	21
Overall Abundance.....	21
Larval Parasitism.....	23
Pupal Parasitism.....	28
Egg Parasitism.....	28
Hyperparasitism.....	28
Host Size Relationships.....	30
Seasonal Distribution and Overwintering.....	35
<u>Apanteles aristoteliae</u>	37
<u>Meteorus argyrotaeniae</u>	39
<u>Phytodietus vulgaris</u>	40
<u>Oncophanes americanus</u>	41
<u>Enytus eureka</u>	41
<u>Diadegma</u> spp.....	42
Parasitoids Reared from Other Tortricids on Caneberries.....	42
The Obliquebanded Leafroller.....	43
The Omnivorous Leaf-tier.....	45

<u>Archips rosanus</u>	47
General Discussion.....	47
Laboratory Studies.....	51
Adult Longevity.....	51
Laboratory Rearing.....	51
Developmental Periods.....	53
<u>Apanteles aristoteliae</u> ; Development at Different Temperatures.....	56
<u>Phytodietus vulgaris</u> ; Life History and Diapause Characteristics.....	62
CONCLUSION.....	73
SUMMARY.....	73
VI. ORANGE TORTRIX OVIPOSITION AND EGG DEVELOPMENT.....	78
INTRODUCTION.....	78
MATERIALS AND METHODS.....	79
Oviposition Behavior.....	79
Egg Development at Constant Temperatures.....	80
Egg Development under Field Conditions.....	81
Estimation of Thermal Constants.....	81
RESULTS AND DISCUSSION.....	82
Oviposition Behavior.....	82
Egg Development at Constant Temperatures.....	87
Egg Development under Field Conditions.....	90
Estimation of Thermal Constants.....	92
Factors affecting Prediction of Egg Hatch....	95
Emergence Patterns.....	96
Interval Between Emergence and Mating;	
Flight Temperature Threshold.....	98
Oviposition Activity.....	99
SUMMARY.....	100
BIBLIOGRAPHY.....	102
APPENDICES.....	108

LIST OF FIGURES

Figure

- | | | |
|---|---|----|
| 1 | Relationship of percent orange tortrix larvae parasitized to average host density and classification into high and low density infestations; seven caneberry fields 1981, one field 1980. | 26 |
| 2 | Contribution of six parasitoid species to total orange tortrix parasitism by size class collected for high density (left) and low density (right) infestations. | 36 |
| 3 | Seasonal representation of red raspberry bloom and harvest and life stages of four tortricid species in western Oregon. | 49 |
| 4 | Cumulative emergence of <u>Apanteles aristoteliae</u> as observed from Woodland, WA. 1981 (points); and predicted by PETE phenology model (solid lines). | 60 |
| 5 | Percent diapause obtained for different larval stages of <u>Phytodietus vulgaris</u> transferred from long days (LD 16:8) to short days (LD 10:14) at 20°C. | 70 |
| 6 | Oviposition record of orange tortrix adults caged in the field at Corvallis, OR. on July 14, September 11, and October 10, 1981; with record of daily temperature extremes and precipitation. | 84 |
| 7 | Orange tortrix cumulative percent oviposition (A) and average egg mass size (B), combined for three replicates; July 14, September 11, and October 10, 1981, Corvallis, OR. | 85 |
| 8 | Development rate of orange tortrix eggs in relation to constant temperature. | 89 |

LIST OF TABLES

<u>Table</u>	<u>Page</u>
1 Orange tortrix parasitoid study: Description of sampling locations and frequency.	11
2 Classification of orange tortrix larvae by sizes through head capsule width measurements (mm).	15
3 Summary of parasitoids reared from the orange tortrix collected in cultivated <u>Rubus</u> spp., Willamette Valley, OR, 1980-1981.	22
4 Abundance measures of orange tortrix larval parasitoids averaged for 22 samples collected and reared from caneberries, 1980-1981.	24
5 Record of orange tortrix pupal parasitoids reared.	29
6 Number of parasitized orange tortrix larvae on <u>Rubus</u> spp., Willamette Valley, OR 1980-1981.	31
7 Host size classes emerged from by seven orange tortrix parasitoids.	32
8 Seasonal and overwintering characteristics observed for some orange tortrix parasitoids, collected in caneberries, Willamette Valley, OR 1980-1981.	38
9 Parasitization record for <u>Choristoneura rosaceana</u> collected in <u>Rubus</u> spp., Willamette Valley, OR, 1980-1981.	44
10 Parasitization record for <u>Cnephasia longana</u> collected in <u>Rubus</u> spp., Willamette Valley, OR, 1980-1981.	46
11 List of alternate hosts of some common orange tortrix parasitoids.	48
12 Adult longevity of four orange tortrix parasitoids; 21 \pm 1.5°C, 60 \pm 15% R.H.	52
13 Development periods of laboratory reared parasitoids of the orange tortrix at 20 \pm 1°C and LD 16:8.	54
14 Duration of developmental stages (days) of <u>Apanteles aristoteliae</u> as related to temperature.	57

<u>Table</u>		<u>Page</u>
15	Regression equations and thermal constants for rate of development of <u>Apanteles aristoteliae</u> in relation to temperature.	58
16	Development periods of life stages of nondiapausing <u>Phytodietus vulgaris</u> at $21 \pm 1^{\circ}\text{C}$ and head capsule measurements of larval instars.	64
17	Summary of preliminary experiments on diapause termination of <u>Phytoditus vulgaris</u> .	67
18	Effects of transferring different developmental stages of <u>Phytodietus vulgaris</u> from short to long day photoperiods; measured as interval to pupation, $20 \pm 1^{\circ}\text{C}$.	71
19	Orange tortrix field oviposition on caged red raspberries; Corvallis, OR 1981.	86
20	Percent hatch and development period for orange tortrix eggs taken from females held at 20°C and incubated at various temperatures.	88
21	Percent hatch and developmental period for field incubation of orange tortrix eggs; Corvallis, OR 1981.	91
22	Orange tortrix egg development: Degree day accumulations calculated for five temperature thresholds and three methods of degree day summation; Corvallis, OR.	93
23	Prediction of orange tortrix egg hatch: thermal constants estimated from linear regression (laboratory data) and by lowest coefficient of variation (field data); Corvallis, OR 1981.	94
24	Emergence of overwintering generation orange tortrix collected at Woodland, WA 1981.	97

ORANGE TORTRIX: PARASITOID COMPLEX AND THERMAL CONSTANTS FOR EGG HATCH

I. INTRODUCTION

The orange tortrix, Argyrotaenia citrana (Fernald) is a periodic pest of bramble fruits (Rubus spp.) and other fruit crops in the Pacific Northwest and California. It is primarily a problem in cane fruits as a contaminant at harvest in machine-picked fruits. The orange tortrix rarely causes direct fruit damage. It normally prefers new vegetative bud or leaf growth which it webs with silk. Usually it is the first larval brood which causes contamination of red raspberry varieties, Rubus ideaus L. during harvest from late June through early August.

Traditionally, chemical control is only partially effective against the orange tortrix due to the asynchronous development of its life stages. This is attributed in part to the lack of a winter diapause in all overwintering larval stadia. Also, the use of insecticides to control this species is limited because of the coincidence of bloom with the hatch of a large proportion of the first generation. Effective insecticides at this time are lethal to the honeybee, Apis mellifera L., essential to pollination and yield of R. ideaus. Although the bacterial insecticide Bacillus thuringiensis Berliner is registered and will control the orange tortrix with safety to bees, time of application to early instar larvae is crucial, and available formulations are susceptible to environmental degradation (Cantwell and Franklin 1966, Griego and Spence 1978).

Natural control by parasitoids has perhaps been a primary factor determining the abundance of the orange tortrix (Johansen 1978). However, literature is lacking in the biological and regulatory functions of orange tortrix parasitoids. Therefore, a survey of the parasitoids which attack the orange tortrix on caneberries was conducted in this study. Particular attention was devoted to the relative abundance of the species in the parasitoid complex on different larval stages as well as their developmental rates at a constant temperature, overwintering habits, adult longevity, and alternate larval hosts in caneberries. Additional studies on the life history of two important species in the complex, Apanteles aristoteliae Vier. and Phytodietus vulgaris Cress. were also conducted.

The purpose of this study was twofold. The first was to document the parasitoid species associated with orange tortrix populations. The second was to determine the developmental threshold temperature and thermal unit requirement for the egg hatch of the orange tortrix under field conditions. To corroborate this information, ovipositional activity was investigated in field cages to refine the interval between pheromone trap catches and oviposition.

This study will provide information for further development of an integrated approach to management of A. citrana in cane fruits. A knowledge of the bionomics and life histories of its parasitoid complex can serve both as a basis for increased grower awareness of

natural control, and as groundwork for future studies on conservation and enhancement of these beneficial insects. Additionally, a model predicting the phenological development of the orange tortrix would enhance the selection and timing of insecticides while affording pollinator safety.

II. LITERATURE REVIEW

Taxonomy

The orange tortrix, Argyrotaenia citrana (Fernald) is placed in the tribe Archipini of the family Tortricidae. C. H. Fernald first described the species in 1889 and placed it in the genus Tortrix. However, August Busck placed it in the genus Argyrotaenia in 1936 where it has since remained. Powell (1964) discussed the synonymy of A. citrana (Fernald) and franciscana (Walsingham). He concluded that the two be regarded as separate species, even though hybridization can occur wherever their distribution overlaps. Additionally Powell noted that A. franciscana is a native of California's central coast; Lupinus spp. probably being among its preferred hosts. He also stated that the apple skinworm is not the species, A. franciscana (Walsingham), but is a variety of A. citrana. This would indicate that several published studies on the apple skinworm, including those by Essig (1926), Penny (1921), and Bartges (1951) were in error as to species name.

Description of Life Stages

Orange tortrix adults are variable in size, color and markings. Females measure from 10.5 to 12 mm in length, males are slightly smaller. Generally, the forewings vary in shades of orange, brown, and tan with dark brown transverse markings which predominate as median saddles in the females but are often reduced in males, which

usually possess more prominent costal spots. The whitish hind wings tend to be greyish posteriorly. A complete description of the adults can be found in Powell (1964).

Head capsules and prothoracic shields of larvae are light brown. Body color varies from a yellow-green, usually observed for larvae feeding on young plant growth, to grey or brownish. Quite often larvae are semi-translucent and can be sexed by the presence of paired testes located mid-posteriorly on abdominal segment 5 in the males. Length usually ranges from 1.75 mm for first instar larvae to 11 mm for fifth instar larvae (Lange 1936). As many as seven instars which may reach a length of 14 mm were observed by Basinger (1938) who suggested that suboptimal conditions may be a factor leading to additional molts.

Eggs are flattened, oval, and finely reticulate. They measure ca. 0.9mm x 0.7mm and overlap in masses numbering from 7 to more than 80 (Basinger 1938).

Pupae as described by Lange (1936) are a dark, chestnut brown color 8-9 mm in length. Usually a fine silk cocoon is spun just prior to pupation.

Distribution and History as a Pest

Originally reported from southern California on oranges in 1894, the orange tortrix is now distributed primarily along the Pacific coast of North America from the Baja peninsula to British Columbia. The list of known host plants has grown to more than 80 species

(Powell 1964, Johansen and Breakey 1949, Basinger 1938). Following is a list of crops in California which have been recorded as suffering some injury, and the year in which damage was first recorded: Orange, Citrus sinensis 1894 (Coquillett 1894), various greenhouse plants, including Rosa sp., Begonia sp., Asparagus spp., Acacia sp., Eucalyptus sp., and Geranium sp. 1910 (Quayle 1910); apple, Malus pumila 1914 (Penny 1921); monterey pine, Pinus radiata 1933 (Lange 1936); grapefruit, Citrus paradisi 1938 (Quayle 1938); lemon, Citrus limonia 1946 (Boyce and Ortega 1947); apricot, Prunus armeniaca 1949 (Madsen, Borden and Clark 1953); avocado, Persea americana 1949 (Ebeling and Pence 1957), and grape, Vitis spp. 1968 (Kido, Stafford and McCalley 1971).

Although it is not documented, its introduction to the Pacific Northwest is thought to have been through greenhouse introductions (Powell 1964). It was observed in Washington as early as 1930 (Anon. 1930). Soon afterwards it was reported a pest in greenhouses and in raspberries of the Puyallup region in 1933 (Breakey and Batchelor 1948). Rosensteil (1949) reported it a serious problem on raspberries in Oregon's Willamette Valley by 1947, having been collected in greenhouses and occasionally caneberries several years earlier (Zeller and Schuh 1944). It has also been noted on cultivated grapes in Washington (Rosensteil 1949).

Biology

Various researchers have reported on the biology of the orange tortrix throughout it's known range. Basinger's (1938) study in

southern California was perhaps the most comprehensive for this insect as a pest of oranges. Powell (1964) reviewed work done in California and added observations of his own. Recently, the orange tortrix has been studied in the Salinas Valley of California where it is an important pest of grapes (Kido et al. 1981).

Both Kido et al. (1981), and Basinger (1938) reported orange tortrix larvae to have a lower developmental threshold temperature of around 6°C. (43°F.) and a higher developmental threshold of about 32°C. (90°F.) These developmental limits perhaps restrict its occurrence in California to the cooler, coastal areas (Basinger 1938). Successive broods greatly overlap in Oregon and Washington and several generations per year have been suggested (Breakey and Batchelor 1948). The larvae overwinter in various immature stages, but primarily as larger larval instars (Powell 1964). No diapause is evident, and larvae will feed on cane buds and outer green cane surfaces on warmer winter days (Breakey and Batchelor 1948, Rosensteil 1949). From Basingers' temperature - developmental rate studies (1938), estimated developmental thresholds and thermal unit requirements have been calculated for the egg, larval and pupal stages (Appendix 1). Larvae prefer new leaf growth which is webbed together furnishing them with food and shelter (Basinger 1938, Breakey and Batchelor 1948). Pupation takes place on raspberries either in the terminal leaves where the larvae last fed, in dead leaves tangled among canes, or on the ground (Rosensteil 1949). Mating and oviposition occur in the

laboratory within two or three days after emergence (Basinger 1938). The recorded average fecundity was 276 eggs/female by the same author. Smooth surfaces are preferred for oviposition, and on raspberries usually the upper leaf surfaces are chosen (Rosensteil 1949). Orange tortrix have been laboratory reared on artificial diets for up to 30 generations (Coudriet 1970). Sex pheromone components have been identified, tested (Hill et al. 1975) and are currently available for use in monitoring programs.¹

Parasitoids

Like many other tortricine moths which have been extensively studied, the orange tortrix is known to be attacked by numerous parasitoids. These include 24 species listed from the Hymenoptera catalog (Krombein et al. 1979) and Tachinidae catalog (Arnaud 1978) as well as other sources (Basinger 1935, Johansen and Breakey 1949, Rosensteil 1949, Breakey 1951, Kido et al. 1981). None of the species are known to be introduced, and no attempt has been made to introduce or redistribute these or other species to control the orange tortrix. Comparisons among studies indicating relative abundance of various species do show differences in geographical range of important members in the complex. The ichneumon Exochus nigripalpus subobscurus Walker for example, is an important member of the complex in California (Basinger 1935, Kido et al. 1981), but has not been collected from

¹Zoecon Corporation, Palo Alto, California.

Washington or Oregon (Townes and Townes 1959). Although other Exochus species occur in Oregon, none have been recorded from the orange tortrix. The braconid Hormius completus (Provancher) is also a major parasitoid in California but has not been recorded from Oregon or Washington. Conversely, the braconids Meteorus argyrotaeniae Johansen, Oncophanes americanus (Weed) and one ichneumonid, Phytodietus vulgaris Cresson, have been recorded in the Pacific Northwest (Breakey 1951) but not from California. M. argyrotaeniae was credited to be a major factor in suppressing an infestation of the orange tortrix in the Puyallup Valley of western Washington. There the parasitization rate by M. argyrotaeniae reached nearly 100 percent by 1950 (Breakey 1951).

The braconid Apanteles aristoteliae Vierick, which has been recorded in most orange tortrix parasitoid studies, is a dominant species in both southern California and Oregon (Anonymous 1926, Basinger 1935, Rosensteil 1949).

Despite numerous reports either demonstrating or alluding to the importance of parasitoids in regulating orange tortrix populations, little information exists on their biologies (Anonymous 1926, Basinger 1935, Breakey 1951, Rosensteil 1956, Madson and McNelly 1961, Kido et al. 1981).

III. PARASITOID COMPLEX

MATERIALS and METHODS

Sample Locations

In order to fulfill the objective of evaluating the contribution of orange tortrix parasitoids, several caneberry fields representing a variety of conditions were sampled. These included different caneberry spp. and varieties, geographical location, season, method of harvest and type and number of insecticide applications received.

A major constraint limiting standardization of sampling techniques was that of locating infestations large enough to sample on a regular basis. Also, the long distance to the few locations which were found to have sizeable populations of orange tortrix larvae restricted the number and size of samples. Several fields that initially had substantial populations for larval collections would subsequently be nearly void of orange tortrix, presumably because of high natural mortality rates. Characteristics of fields visited at least twice and found to have populations of orange tortrix large enough to yield information on parasitoid abundance are given in Table 1. Included in this list are five locations where primarily red raspberries were grown. Two of these fields were machine harvested. Also, two evergreen blackberry fields on the alternate year harvesting system were sampled. Tsugawa farms in Woodland, Washington had the largest populations observed in this study and were the only fields to consistently yield salient biological information on the parasitoid

Table 1. Orange tortrix parasitoid study: Description of sampling locations and frequency.

Grower	County, State	Locality, dist. from Corvallis	Crop, harvest method	Acreage	No. of insecticide applications ^a	No. occasions sampled	No. of samples >12 ^b
George Tsugawa	Cowlitz Washington	Woodland 120 mi. N.	red rasp. machine	23	2(1980) 3(1981)	12(1980) 7(1981)	8(1980) 7(1981)
Mike Hopfer	Marion Oregon	St. Paul 70 mi. N.	red rasp. machine	8	2	5	4
Ralph Smith	Washington Oregon	Scholls 80 mi. N.	red rasp. hand	8	0	2	2
Homer Twedt	Benton Oregon	Corvallis -	red rasp. hand	4	0	5	3
Oregon State	Benton Oregon	Corvallis -	red rasp. hand	0.2	0	7	2
Joe Brunner	Lane Oregon	Junction City 30 mi. S.	blackberry machine	30	0	3	1
B and B Farms	Polk Oregon	Salem 38 mi. N.	blackberry machine	60	0	2	1

^a year of study, exclusive of bacterial insecticides.

^b number of sampling occasions in which more than 12 orange tortrix larvae were collected.

complex. This location was visited several times in spring and autumn to develop information on seasonal abundance and overwintering characteristics of the parasitoids present. Red raspberry or evergreen blackberry fields owned by Mike Hopfer of St. Paul, Oregon were sampled 4 times in 1981. Here, too, relatively large populations of orange tortrix larvae were collected. At both locations, berries were machine harvested and received 2 or more insecticide applications per year.

Five additional locations were sampled which differed from the two mentioned above in terms of population density and insecticide application. These included two hand-harvested red raspberry fields; one in Corvallis, Oregon and the other in Scholls, ca. 80 miles north of Corvallis. Conventional insecticides were not applied to these fields during the year of study; however, the Scholls field received a single application of Bacillus thurengiensis. A non-commercial, one year old, red raspberry plot located at the O.S.U. entomology experimental farm was also used as a collection site for orange tortrix larvae. Finally, two machine-harvested evergreen blackberry fields were visited which were located in Salem and Junction City, Oregon. In both cases collections were made from the non-fruit-bearing (primocane) portions of these fields. Nearby sections had been sprayed with organo-phosphate or carbamate insecticides and harvested, but the non-bearing portions were relatively undisturbed during the 1981 season.

Host Collection and Rearing

Larval stages of the orange tortrix were primarily collected by a visual search method. This involved walking caneberry rows and inspection for webbed terminal leaf clusters in which larvae feed. Later instar larvae represented the bulk of the collections because of their more conspicuous feeding sites indicating a bias in using this procedure. When a feeding site was located, the entire leaf cluster was removed and the leafroller species determined before placing in a plastic pint container. Sampling dates were chosen to give a relative indication of seasonal larval density. Efforts were made to equally distribute search time in all portions of fields sampled. However, it was often discovered that the larvae were unequally distributed. Approximately five to ten minutes of each sampling period was devoted to searching upper leaf surfaces for egg masses for analysis of potential egg parasitoids. However, only two masses were detected and no other method of adequately sampling them was determined.

Once brought to the laboratory, field collected larvae were removed from the leaf clusters and placed individually on artificial diet in 22 ml plastic cups with paper lids. The diet used was similar to that developed for western spruce budworm (Lyon et al. 1972), although it differed slightly by using a commercially prepared mixture¹ for convenience. The exact recipe used did not appear to

¹Vanderzant-Adkisson diet. ICN Nutritional Biochemicals, Cleveland, Ohio.

be of great importance, since normal imagos were obtained for several slightly different wheat-embryo based diets.

Head capsules widths of all orange tortrix larvae were measured without anesthesia using a dissecting microscope fitted with an ocular micrometer. Most larvae were measured within ± 0.05 mm. Several hundred were measured to an accuracy of ± 0.025 mm. Of these, the measurements of 298 non-parasitized larvae were compiled and used as the primary basis for size class determination (Table 2).

Classification into size classes was based on the assumption that five instars normally occur during the summer, whereas up to six can occur during winter. The first four head capsule size classes did not overlap and corresponded closely with instars reported by Schwartz and Lyon (1970). Fifth and subsequent instar measurements overlapped, however. A potential reduction in size due to parasitization itself also may occur (Vinson and Iwantsch 1980). Therefore the actual number of molts could not be determined, as found for several other lepidoptera not having a fixed number of instars (Frick and Wilson 1981). The term "size class" rather than "instar" will be used, then.

Three other tortricid species were encountered during the course of this study. They too were collected and reared for parasitoids as previously described. Of these, the obliquebanded leafroller (OBLR) was the most common. In fact, OBLR was occasionally more abundant than the orange tortrix, but only a portion of these larvae sampled were reared. Head capsule measurements were taken on ca. half of the more than 240 OBLR larvae reared. Size class determination for the others

Table 2. Classification of orange tortrix larvae by sizes through head capsule width measurements (mm).

Size Class	Males			Females			Both sexes		
	n	Range	Mean	n	Range	Mean	n	Range	Mean
I	-	-	-	-	-	-	4	.20-.21	.20
II	-	-	-	-	-	-	7	.30-.36	.33
III	-	-	-	-	-	-	23	.40-.56	.47
IV	28	.60-.80	.69	58	.62-.92	.75	86	.60-.92	.73
V	58	.84-1.04	.97	59	.94-1.20	1.10	-	-	-
VI	22	1.10-1.30	1.15	39	1.22-1.41	1.29	-	-	-

was by estimation. The two other leafroller species infrequently collected were the omnivorous leaftier, Cnephasia longana (Weed) and the european (filbert) leafroller, Archips rosanus Linnaeus.

Leafroller larvae and pupae of all four species were reared almost exclusively in Percival® incubators at a temperature of $20.0 \pm 1.0^{\circ}\text{C}$ and photoperiod regime of light:dark (LD) 16:8 hr. Some larvae were maintained at room conditions with natural lighting during a portion of the 1980 season.

All field collected specimens were observed daily. Data on parasitoid cocoon formation and emergence, as well as death, pupation and emergence of the host was recorded. Adult parasitoids were either used for further studies or preserved for identification.

Parasitoid identifications were obtained from various sources. Scientists at the United States National Museum in Beltsville, Maryland provided most of the determinations for the Tachinidae, Braconidae, Chalcididae, and Trichogrammatidae. The Ichneumonidae were determined at the generic level by H. K. Townes¹. Species names, if determined, were made by myself with help from Torolf Torgersen². Conrad Loan³ identified the ichneumonid Phytodietus vulgaris Cresson.

¹ Entomological Institute of America. Ann Arbor, Michigan.

² USDA Forestry Sciences Laboratory, Corvallis, Oregon.

³ Agriculture Canada, Ottawa Research Station. Ottawa, Canada.

Laboratory Studies

Adult Longevity

In order to obtain a relative estimate of the adult longevity of some of the orange tortrix parasitoids, newly emerged adults were placed in 20x20x40 cm screened cages. Honey served as a food source and was streaked in small droplets along plastic container lids or wax paper. This was replaced twice weekly. Cotton saturated with distilled water was provided in 22 ml plastic cups. The cages were maintained at $21 \pm 1.5^{\circ}\text{C}$. and $60 \pm 15\%$ R.H. Different species were separated. Males and females were caged together. Parasitoid adults were checked daily for survival under these conditions. At least 7 individuals were observed in estimating average longevity for each species.

Laboratory Rearing

An attempt was made to rear several of the common parasitoid species obtained from the orange tortrix. The procedure used was to place one to several laboratory - reared orange tortrix larvae overnight in cages containing one or more of the female parasitoids. The next morning these larvae were placed on artificial diet and kept in an incubator at $20.0 \pm 1.0^{\circ}\text{C}$ and $80 \pm 10\%$ R.H. The range of different host instars used was roughly matched to sizes observed for field collected hosts. Because Meteorus argyrotaeniae Johansen did not respond to hosts reared on artificial diet, they were provided with hosts contained in red raspberry leaf terminals.

Developmental Periods

Orange tortrix larvae presumed parasitized were placed individually on artificial diet and reared under the same conditions as field collected orange tortrix, 20°C and LD 16:8 hr. Daily observations were made and events recorded regarding parasitoid cocoon formation, adult emergence, and sex. The number of individuals used for developmental interval estimates varied from a minimum of 13 for M. argyrotaeniae to 34 for Phytodietus vulgaris.

For some species not successfully reared in the laboratory, an estimation of developmental time was still obtained. This was based on the average time in the cocoon stage plus maximum time in the egg-larval stage of parasitoids reared from field collected hosts.

Apanteles aristoteliae; Development at Different Temperatures

A. aristoteliae was the most common orange tortrix parasitoid reared in this study. Its developmental response to temperature was investigated to provide information towards estimating its thermal constant values and maximum number of annual generations.

Parasitization was achieved by placing F₁ orange tortrix larvae in cages for 3 or 4 hours which contained A. aristoteliae adults. Conditions were the same as for the adult longevity study. Following parasitization, larvae were placed individually in 22 ml plastic cups containing artificial diet and into one of six Percival® incubators set at 12.0, 16.7, 20.0, 24.0, 28.0, and 30.0°C. Photoperiod was LD 16:8 hr. Humidity was controlled at $77 \pm 2\%$ R.H. by placing the cups into tight sealing plastic freezer containers containing a potassium

hydroxide solution (Solomon 1951). A minimum of 20 larvae for each temperature were used except at 12°C., at which only 14 were successfully reared. Larvae were observed daily for parasitoid cocoon formation, emergence, and death.

Using linear regression, estimates of the developmental threshold temperature and thermal unit requirements were obtained for egg + larval, pupal, and egg-to-adult development by the methods given in Campbell et al. (1974). These values were then used to estimate the maximum number of generations per year. This was accomplished by using field data and a number of assumptions about the biology of A. aristoteliae (Appendix 6) for simulation of its phenology with the PETE model (Welch et al. 1978).

Phytodietus vulgaris; Life History and Diapause Characteristics

The ichneumonid P. vulgaris was a widespread and relatively abundant species in the complex. Further studies on the life history of P. vulgaris were conducted because it was easily reared in the laboratory and also because it is an external parasitoid and thus had readily observable development.

When it was accidentally discovered that P. vulgaris underwent diapause as a mature larvae following cocoon construction, preliminary experiments were begun to determine how photoperiod, and to a lesser extent, temperature influence initiation and termination of diapause. Photoregime and temperature were controlled by means of Percival®

incubators. F₁ and F₂ P. vulgaris reared from parents obtained at the Woodland, Washington location were used. Hosts were F₁ orange tortrix reared on artificial diet.

To determine the developmental stages sensitive to photoperiod induced diapause, information on the number of instars and duration of each stadium was required. This was done by taking head capsule measurements daily for a number of developing P. vulgaris larvae. The method used was the same as that described for measuring orange tortrix head capsule widths. No anesthesia was used and care was taken not to disrupt the externally feeding parasitoid or its host. Head capsules of final instar P. vulgaris were very difficult to measure in this way so 14 were preserved in 70% alcohol and measured at a later time.

The experimental procedure used to determine stages sensitive to diapause induction consisted of initially rearing larval P. vulgaris under long day conditions, LD 16:8 hr. Then larvae of different instars were subjected to short day (diapause-inducing) conditions, LD 10:14 hr. A greater number of third, fourth, and fifth instar P. vulgaris were transferred because these were the stages believed to be most sensitive to photoperiod. The criterion used for the recognition of diapause was that development would cease at the mature larval (or pupal) stage whereas for non-diapausing larvae, development was continuous through the pupal stage within four or five days following cocoon formation.

RESULTS AND DISCUSSION

Overall abundance

Of the 24 orange tortrix parasitoid species previously reported, 12 were reared in this study (Table 3). Additionally, 4 species for which the orange tortrix represents a new host record were obtained. Two other species may represent new parasitoid rearings but should conservatively be considered as in doubt primarily because only one individual each of these species was reared and the host was not positively identified. These were; Temelucha sp., and Voria ruralis (Fallen), both of which were reared from small overwintering orange tortrix larvae. Although Temelucha is known to parasitize other tortricids, V. ruralis is known from only larger lepidopteran species, mostly of the family Noctuidae.

Some mention should be made of the extent to which the taxonomic status of these species was determined. For the Ichneumonidae, species names could not always be obtained since presently no authority is known that will provide determinations. In the case of the Diadegma spp., H. Townes indicated after inspection that two or three species of this genus are involved. Both past studies and comparison with specimens in the O.S.U. entomology museum indicate that probably most of these are of the species D. interruptum pterophorae (Ashmead). No morphological or biological basis for separating pterophorae from other species in the Diadegma complex could be made so they will be dealt with as Diadegma spp. in the

Table 3. Summary of parasitoids reared from the orange tortrix collected in cultivated Rubus spp., Willamette Valley, OR, 1980-1981.

Species	Determined by	Family	Number reared	Mode ^a
<u>Apanteles aristotaliae</u> Viereck	P. Marsh	Braconidae	119	Larval
* <u>Meteorus argyrotaeniae</u> Johanson	P. Marsh	Braconidae	107	Larval
<u>Phytodietus vulgaris</u> Cresson	C. Loan	Ichneumonidae	42	Larval ectoparasitic
<u>Enytus eureka</u> (Ashmead)	L. Coop	Ichneumonidae	27	Larval
<u>Diadegma</u> spp.	H. Townes	Ichneumonidae	26	Larval
<u>Oncophanes americanus</u> (Weed)	P. Marsh	Braconidae	22	Gregarious, larval ectoparasitic
* <u>Parania geniculata</u> (Holmgren)	L. Coop	Ichneumonidae	12	Larval-pupal
* <u>Meteorus dimidiatus</u> (Cresson)	L. Coop	Braconidae	6	Larval
<u>Pseudoperichaeta erecta</u> (Coquillett)	D. Wilder	Tachinidae	4	Larval, Larval-pupal
<u>Meloboris</u> sp.	H. Townes	Ichneumonidae	1	Larval
+ <u>Temelucha</u> sp.	H. Townes	Ichneumonidae	1	Larval
+ <u>Voria ruralis</u> (Fallen)	C. W. Sabrosky	Tachinidae	1	Larval
<u>Meteorus trachynotus</u> Viereck	L. Coop	Braconidae	1	Larval
<u>Stictopisthus</u> sp.	H. Townes	Ichneumonidae	3	Hyperparasitic on <u>Apanteles</u> larva
* <u>Spilochaetis</u> sp.	E. E. Grissell	Chalcididae	2	Pupal, primary and hyperparasitic on <u>Apanteles</u> cocoon
<u>Itoplectis quadricingulata</u> (Provancher)	G. Ferguson	Ichneumonidae	3	Pupal
* <u>Elachertus</u> sp.	P. Hanson	Eulophidae	1	Larval, ectoparasitic
<u>Trichogramma</u> sp.	D. R. Vincent	Trichogrammatidae	1	Egg

+ Relationship with host not certain.

* New host record.

^a Solitary and endoparasitic unless otherwise noted.

remainder of this thesis. According to the Hymenoptera catalogs; Nepiera fuscifemora Graf. is a known parasitoid of the orange tortrix, and that this name is distinct from the genus Meloboris, for which Townes considered Nepiera to be a synonym. It is likely, but not certain that the Meloboris sp. named as a parasitoid of both the orange tortrix and Archips rosanus in this study is actually N. fuscifemora.

Larval Parasitism

Abundance measures for the larval parasitoids reared from the 22 samples for which a minimum of 11 and mean of 42 larvae were collected, are presented in Table 4. Measurements of total percent parasitism, percent of samples collected from, and average percent parasitism when present are included. Data from these 22 samples from which these measurements were calculated are contained in Appendix 2.

A total parasitization rate of 34% was observed for the 918 larvae reared, with individual samples ranging from 4.3% to 100%. Two species; Apanteles aristoteliae and Meteorus argyrotaeniae, accounted for 63% of all parasitoids reared. Both species were present at all red raspberry locations sampled. Four less abundant species, Phytodietus vulgaris, Diadegma spp., Enytus eureka, and Oncophanes americanus, made up an additional 30% of the parasitoids reared in these samples. The species Parania geniculata and Meteorus dimidiatus plus five others accounted for the remaining 7%.

Table 4. Abundance measures of orange tortrix larval parasitoids averaged for 22 samples collected and reared from caneberries, 1980-81.

Species	Number reared	Total % parasitism	% of samples present in	Ave % parasitism when present
<u>Apanteles</u> <u>aristoteliae</u>	103	11.2	72.7	15.4
<u>Meteorus</u> <u>argyrotaenia</u>	94	10.2	50.0	15.1
<u>Phytodietus</u> <u>vulgaris</u>	36	3.9	36.4	8.7
<u>Enytus</u> <u>eureka</u>	20	2.2	54.5	3.3
<u>Diadegma</u> spp.	22	2.4	22.7	9.4
<u>Oncophanes</u> <u>americanus</u>	16	1.7	27.3	14.4
<u>Parania</u> <u>geniculata</u>	9	1.0	13.6	4.0
<u>Meteorus</u> <u>dimidiatus</u>	5	0.5	13.6	2.2
Others	8	0.9	27.3	2.3
Totals	312	34.0	---	---

The percentage of samples each species was reared from gives a relative estimate of how widespread these species are. Both A. aristoteliae and M. argyrotaeniae were present in at least half of all samples taken, and they can be considered among the most widespread as well as most abundant species reared. Enytus eureka differed in that it was relatively widespread, having been present in 54.5% of the 22 samples but was of unusually low abundance at only 2.2% parasitism. Phytodietus vulgaris was similar in being fairly common but usually of limited abundance, when present, except during fall, 1980 in Woodland, WA. (Appendix 2). A much higher contribution of 14.4% parasitism was observed for Oncophanes americanus when it was present in a sample. Given that this species was totally absent from all samples taken from Woodland, WA (Appendix 2), O. americanus is likely to be of higher abundance in the Willamette Valley than the total figures indicate. The reverse was observed for the larval-pupal species Parania geniculata, which was only found during several closely spaced samples from a single season in Woodland, WA. By this evidence it should perhaps be considered a rare or only occasional member of the complex.

When host density, measured as number of larvae collected per hour averaged for each location is considered, some correlation with total percent parasitization is observed. In Figure 1, two general categories of infestation types become evident. The two fields which received an insecticide application at least twice and had large numbers of orange tortrix larvae, had comparatively low average

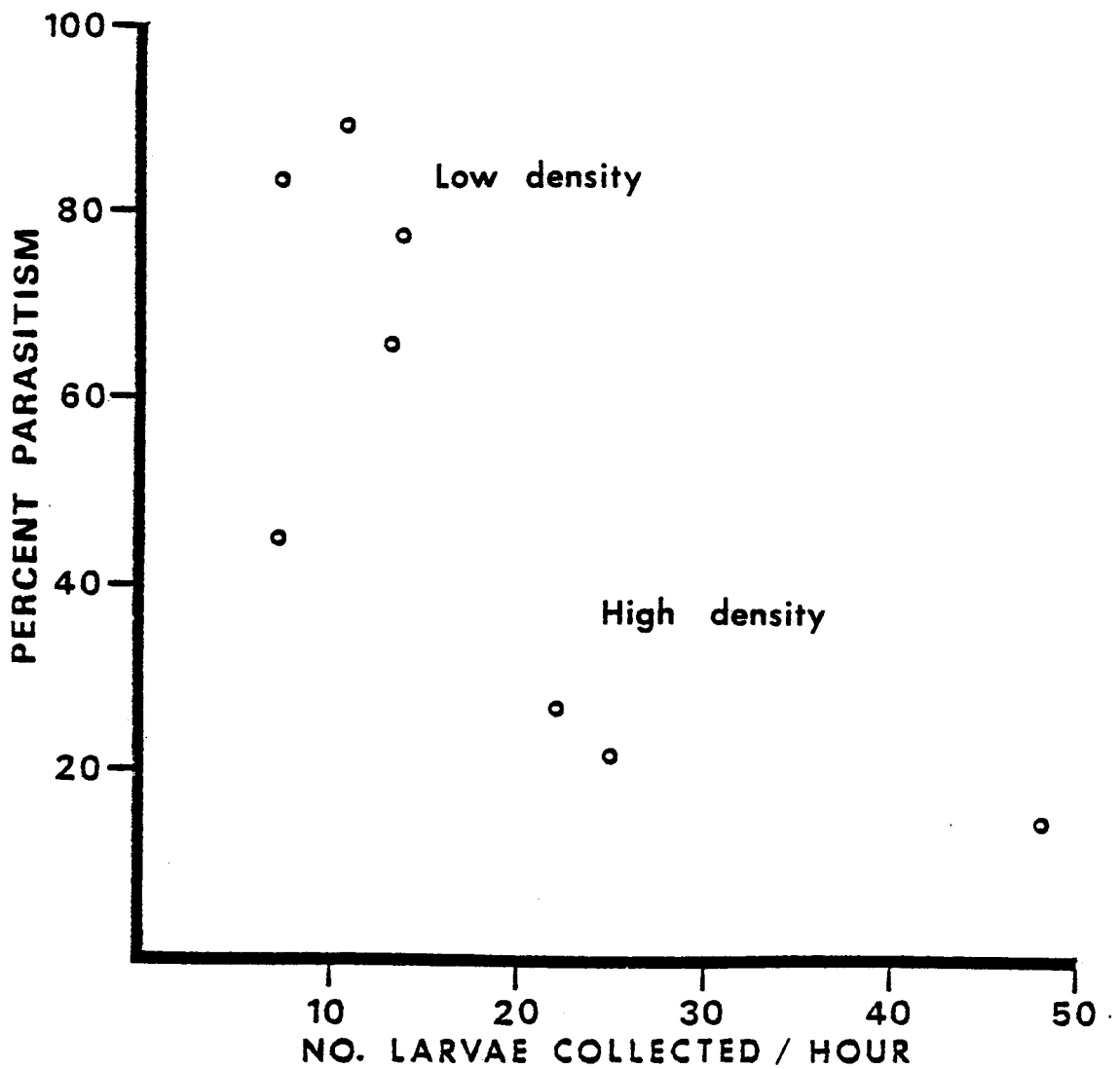


Figure 1. Relationship of percent orange tortrix larvae parasitized to average host density and classification into high and low density infestations; seven caneberry fields 1981, one field 1980.

percent parasitization rates (avg. 20%). The highest percent parasitism reached for any sample at these localities was only 35.0%. The other five locations surveyed in this study were not treated with insecticides and all had relatively low density populations. These had much higher average parasitization rates which ranged from 23.1% to 100% for individual samples and averaged 65.9% overall. Because percentage parasitism was great for fields of low host density, the importance of parasitoids in holding orange tortrix populations to non-epidemic levels is suggested. This was also the interpretation given to similar results obtained in a study of orange tortrix parasitism in two California vineyards (Kido et al. 1981). A key factor analysis on populations of another tortricid, Acleris variana (Fern.) indicated that weather and low parasitism rates were primarily responsible for outbreaks, while late larval parasitism was mainly responsible for population decline (Miller 1966).

Although it seems likely that the usage of insecticides may have been a factor in maintaining epidemic population levels at the Woodland, WA and St. Paul, OR locations because of their impact on natural enemies of the orange tortrix, many other commercial fields are using similar insecticide spray schedules which have not developed such large populations (R. Lalone, pers. comm.) Another explanation for the large populations of orange tortrix maintained at those locations is that the insecticides used did not kill significant proportions of populations which were spread over several life stages.

Pupal Parasitism

Parasitism of orange tortrix pupae was not well documented in this study. Seven individuals in four species were reared from 27 host pupae collected through the visual search method, making up 25.9% parasitism (Table 5). Itoplectis quadricingulata, a cosmopolitan and non host-specific ichneumonid, was the most abundant pupal parasitoid reared. Two others, Parania geniculata and Pseudoperichaeta erecta, were reared from larvae as well as pupae. In addition one Spilochalcis sp. was obtained, probably the same species as was reared from an Apanteles aristoteliae cocoon.

Egg Parasitism

Only two orange tortrix egg masses were collected during this study, neither of which yielded any parasitoids. A large number of egg masses which were potentially subjected to parasitization during the field egg development study also showed no parasitism. A single Trichogramma sp. female was found resting on top of an unparasitized egg mass during this study, however, indicating that egg parasitism may be probable. The orange tortrix has been recorded as a host in the laboratory for Trichogramma minutum Riley (Flanders, 1930).

Hyperparasitism

Only 2 species of hyperparasitoids were reared during this study. This comprised only 1.1% of all parasitoids reared. These were Stictopisthus sp., an ichneumonid and Spilochalcis sp., a chalcid (Table 3). Apanteles aristoteliae Vier. was the primary parasitoid

Table 5. Record of orange tortrix pupal parasitoids reared.

Species	Number reared	%
<u>Itoplectis</u> <u>quadricingulata</u>	3	11.1
<u>Parania</u> <u>geniculata</u>	2	7.4
<u>Pseudoperichaeta</u> <u>erecta</u>	1	3.7
<u>Spilochalcis</u> sp.	1	3.7
Total parasitized	7	25.9
Non-parasitized pupae collected	20	74.1
Total	27	100.0

involved in each case, with Stictopisthus reared as an internal larval hyperparasitoid, eventually emerging from the cocoon of Apanteles, and Spilochalcis emerging from an Apanteles cocoon collected in the field. Hyperparasitism associated with the orange tortrix was also reported to be of little significance by Basinger (1935). Secondary parasitism of pupae may be much more common as was found for OBLR on red raspberries by Schuh and Mote (1948).

Host Size Relationships

Each parasitoid species reared in this study was found to show certain relationships to host size class as indicated by records of apparent host instar at the time of collection (Table 6), and at the time the host is killed (Table 7). Of the six larval parasitoids most commonly reared in this study, two general categories of host size preferences are seen; those which attack small to medium sized orange tortrix larvae and allow development up to medium and large sizes; and those which attack and emerge from midsized and larger hosts.

Although it is often difficult to determine the maximum size of host that will be parasitized, the information obtained in this study is believed sufficient for estimates for four of them. Field rearings of Apanteles aristoteliae indicate that it attacks the second, third, and fourth size classes of orange tortrix larvae. This was also observed in the laboratory rearings in which small fifth "instars" were also successfully parasitized. The majority of the specimens for which head capsules were measured following consumption by A.

Table 6. Number of parasitized orange tortrix larvae on Rubus spp., Willamette Valley, OR 1980-1981.

Species	Host size class ^a						All Instars	%
	I	II	III	IV	V	VI		
<u>Apanteles aristoteliae</u>		8	30	81	1		120	8.9
<u>Meteorus argyrotaeniae</u>			2	38	62	5	107	7.9
<u>Phytodietus vulgaris</u>			1	9	29	3	42	3.1
<u>Enytus eureka</u>	1	6	3	13	4		27	2.0
<u>Diadegma</u> spp.		3	2	17	4		26	1.9
<u>Oncophanes americanus</u>				6	16		22	1.6
<u>Parania geniculatus</u>				4	6		10	0.7
<u>Meteorus dimidiatus</u>		1		3	2		6	0.4
<u>Pseudoperichaeta erecta</u>					3		3	0.2
<u>Meloboris</u> sp.			1				1	0.1
<u>Temelucha</u> sp.		1					1	0.1
<u>Meteorus trachynotus</u>					1		1	0.1
<u>Stictopisthus</u> sp.			2	1			3	0.2
Unknown sp.		1		1			2	0.2
Total all parasitoids	1	19	42	173	128	8	371	
Non-parasitized larvae reared	23	41	161	290	376	88	979	
Total reared	24	60	203	463	504	96	1350	
Percent parasitized	4.2	31.7	20.7	37.4	25.4	8.3	27.5	

^aBased upon instar classifications of non-parasitized field collected larvae.

Table 7. Host size classes emerged from by seven orange tortrix parasitoids.

Species	Size Class ¹			
	III	IV	V	VI
<u>Apanteles aristoteliae</u>	2	49	3	
<u>Meteorus argyrotaenia</u>		5	40	2
<u>Phytodietus vulgaris</u>		2	27	2
<u>Enytus eureka</u>		10	2	
<u>Diadegma spp.</u>		12	8	
<u>Oncophanes americanus</u>		5	14	
<u>Meteorus dimidiatus</u>		4	3	

¹ Based upon size classifications of non-parasitized field collected larvae.

aristoteliae were classified into the fourth size class. It was observed in several specimens parasitized by this species, that a molt occurred which normally would have caused the larvae to be of the fifth instar. An insufficient increase in size, however, produced a measurement equivalent to that of the fourth instar. A similar marked decrease in size due to parasitization by Apanteles fumiferanae Vier. attacking the spruce budworm, Choristoneura fumiferanae (Clem.) was observed by McGugan (1955).

Meteorus argyrotaeniae, generally attacks fourth, fifth and sixth instar orange tortrix larvae and emerges from fifth and sixth instars. Retardation of orange tortrix growth was not observed to occur for M. argyrotaeniae as it had in A. aristoteliae. M. argyrotaeniae emerges from its host without killing it and spins a cocoon nearby.

Oncophanes americanus was exceptional among the complex because it caused a nearly complete paralysis of the larval host, thus stopping development. The adult was observed to parasitize nearly mature larvae; fourth and fifth instar. Much larger, mature larvae of the tortricid Choristoneura rosaceana (Harris) are also parasitized by this species.

Despite the ectoparasitic mode of Phytodietus vulgaris, the host often underwent a normal ecdysis while parasitized by this species, apparently because of its attachment by means of a stalk inserted into the host integument. Since the parasitoids' development could be directly observed, the host size preferences of ovipositioning females

in the field could be ascertained with a high level of certainty. Nearly mature larvae are preferred, although hosts as small as third instars can be utilized.

Diadegma spp. apparently prefer slightly larger hosts than does Enytus eureka. This may explain why the adults of this species are larger than those of the other species. Both may attack very small to medium sized instars and emerge from nearly full grown hosts.

Total parasitization for host sizes collected is also given in Table 6. Percent parasitism was highest (37.4%) for the fourth instar. This is to be expected since all major species in this study were found to develop on this stadium of the host. Twenty-five percent of the fifth size class larvae collected were parasitized, probably because two common species, A. aristoteliae and E. eureka, seldom allow host development to attain this size.

It may be significant that parasitized orange tortrix are, for most species, not removed from the population until pupation has occurred in non-parasitized hosts anyway. The probability of a larva being present as a potential contaminant during harvest, then, does not appear to be greatly reduced even when parasitism is great. Thus the potential for immediate control by inundative releases of larval parasitoids, generally, does not appear to be feasible before and during harvest. This approach may have potential during other times of the year, however. Also the species O. americanus, since it brings about nearly total paralyzation very rapidly, is an exception.

The relatively low percentage parasitism of 8.3% for larvae classified as sixth instar correlates with a general low abundance of parasitoids during spring and late fall, the periods in which these larger larvae were primarily collected.

Figure 2 depicts the percent parasitism by major contributing species by host sizes collected for the two general categories of orange tortrix infestations mentioned previously. Average parasitism in all host size classes was considerably higher for the fields which were found to have relatively low density orange tortrix populations. Inspection of the comparative species composition further reveals that for the most part, all six species were contributing to various degrees in both categories. A partial exception to this was the absence of O. americanus from the Woodland, WA site. For third, fourth, and fifth instars collected, 82% of the difference in total parasitization between high and low density populations is attributable to the differing contributions of only three braconid species; A. aristoteliae, M. argyrotaeniae, and O. americanus. Examination of how insecticide applications, cane maintenance during the winter and other cultural practices affect the survivorship of each of these species could yield insight on how parasitoids should be managed for maximum effectiveness.

Seasonal Distribution and Overwintering

The six most abundant species surveyed appear to be multivoltine. This is based both upon collections made and from their

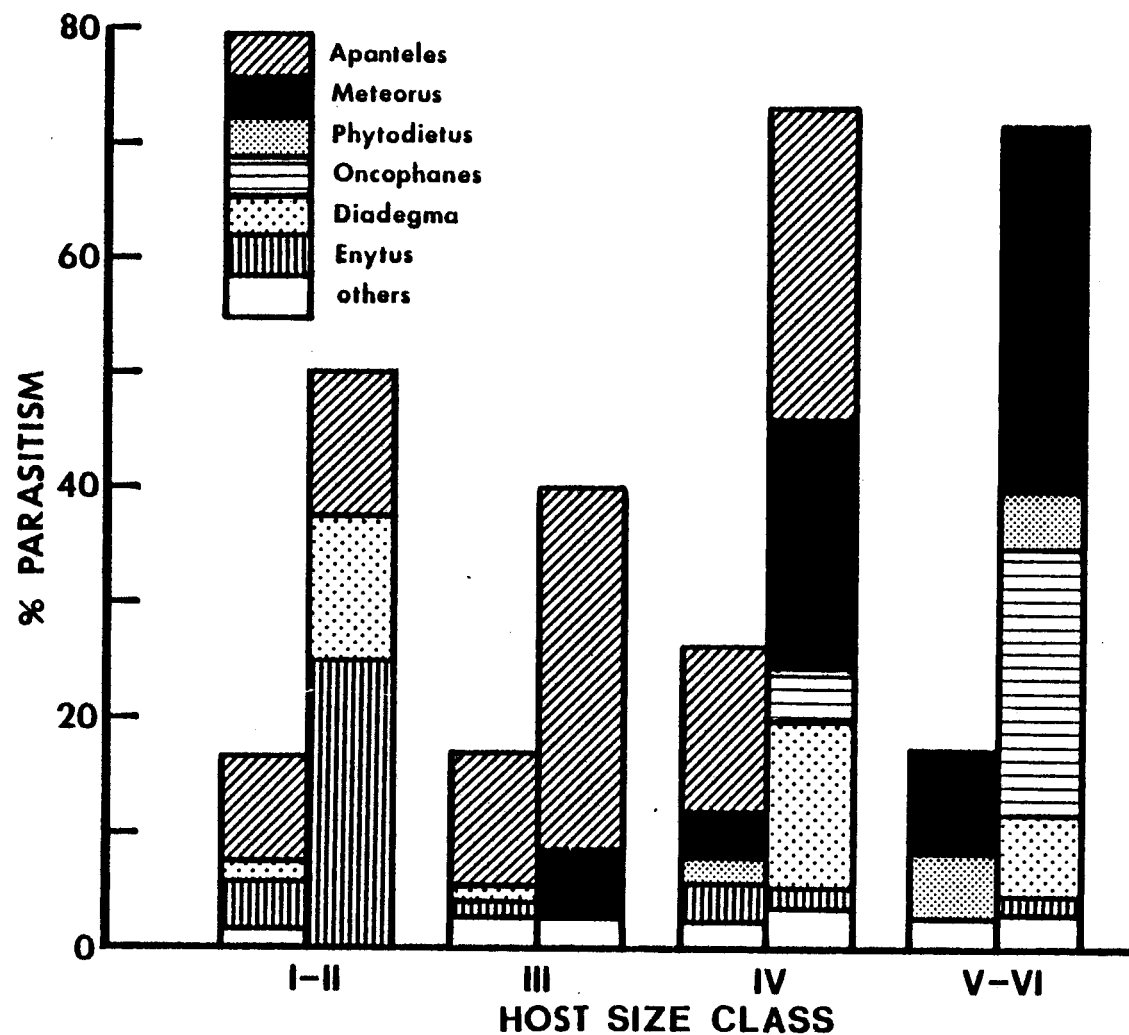


Figure 2. Contribution of six parasitoid species to total orange tortrix parasitism by size class collected for high density (left) and low density (right) infestations.

egg-to-adult developmental intervals, which were shorter than that observed for the host, A. citrana. Evidence pertaining to seasonal distribution and overwintering for each species is reviewed. A summary of the results is presented in Table 8.

Apanteles aristoteliae

Rearing records indicate that this species can be reared from A. citrana at nearly any time of the year. From samples taken in October, November and March, it appears to be capable of overwintering inside of the host. Using comparisons of developmental time to the cocoon stage for different samples helps to establish this. (Appendix 3a,b). For example, two A. aristoteliae reared from A. citrana collected on November 8, 1980 required a mean of 20.0 days to complete egg-larval development and form cocoons, which is 98% of the mean time observed for total egg-larval development in laboratory rearings. This is strong evidence that these particular specimens would have overwintered inside of their host. Specimens collected on October 11 were reared under natural photoperiods and required 46 days to cocoon formation, or 226% of normal egg-larval development. It may be inferred from this that an arrested development other than simple quiescence takes place. The ability to overwinter inside the host is also supported by the long developmental period to cocoon formation remaining for A. aristoteliae collected in March. Leaf litter samples in the spring indicate that pupation occurred from March through May. (see Figure 4, p. 60). Evidence of a first generation in Woodland, WA in 1981 was seen in samples collected from May 26 and June 26 from first generation orange tortrix.

Table 8. Seasonal and overwintering characteristics observed for some orange tortrix parasitoids, collected in caneberries, Willamette Valley, OR 1980-1981.

Species	Months collected ^a	Host generation(s) of greatest abundance ^b	Overwintering capability
<u>Apanteles aristoteliae</u>	March to November	1-3	in orange tortrix larvae
<u>Meteorus argyrotaeniae</u>	March to November	1-2	in orange tortrix larvae
<u>Phytodietus vulgaris</u>	June to November	2-3	mature larvae inside cocoons
<u>Oncophanes americanus</u>	June to September	1-2	mature larvae inside cocoons
<u>Enytus eureka</u>	March to November	-	in orange tortrix and OBLR larvae
<u>Diadegma</u> spp.	April to October	-	in orange tortrix and OBLR larvae

^aNo samples taken from December through February.

^bMonths approximately corresponding to host generation: 1, July; 2, August to September; 3, September to November.

A sample of 37 orange tortrix larvae taken September 18, 1981 near Junction City, Oregon, was 65% parasitized by A. aristoteliae, and 71% of these were within 7 days of cocoon formation in the laboratory. Several collected as cocoons emerged in 3 to 10 days. This result can be interpreted to mean that emergence would be continuing later into October. No evidence of a diapause inside the cocoon was seen when reared under short day conditions. Evidence on the number of generations per year for this species is presented later (pp. 56-61).

Meteorus argyrotaeniae

A few M. argyrotaeniae were reared from late fall and early spring collections of orange tortrix larvae. This indicates that this species has the ability to overwinter inside of the host (Appendix 4a, b). Evidence of a diapause within the host was also observed in two larvae reared under natural photoperiods with a resulting egg-larval development 284% of the average obtained in laboratory rearings. This parasite was not observed to overwinter inside the cocoon, and there is no direct evidence that this occurs, either by short day induced arrested development or by emergence from early season leaf litter samples. First generation immatures were first collected in early May from hosts which were still of the overwintered generation. In general this species was very rarely found in fall collections, indicating that it has a greater impact during the summer, when it was often abundant.

Phytodietus vulgaris

P. vulgaris eggs and larvae were collected from early May through November, although the last indication of oviposition occurred in early October by the stages of development collected. Because of the long oviposition period observed in the laboratory (maximum 45 days) and the relatively short development time (avg. 27 days at 20°C), this ichneumon probably has several greatly overlapping generations per year. Overwintering normally occurs as a mature larva in diapause within a cocoon formed at the site where the host had prepared to pupate. Even though 12 to 19% of the orange tortrix larvae collected in fall 1980 in Woodland, Washington were parasitized by P. vulgaris, none were reared from the orange tortrix at this location the next spring. However, one taken from a leaf litter sample collected March 3 emerged early enough to indicate that overwintered orange tortrix larvae can potentially be utilized. This may reflect an inclination of P. vulgaris for dispersal, a suggestion supported both by its relatively widespread occurrence and low parasitism rates as noted earlier.

In a total of 31 hosts parasitized by P. vulgaris collected from September to November, two of them succumbed to competitors, one each of M. argyrotaeniae and A. aristoteliae. Only eight P. vulgaris-parasitized larvae were collected in June and July. Three of these resulted as M. argyrotaeniae, one as O. americanus, and one was successfully multiple-parasitized by P. vulgaris and M. argyrotaeniae. The high proportion of loss to competitors during summer (62.5%) is

attributable to the higher abundance of those other species during that season. Thus P. vulgaris was both generally more abundant and more successful during the fall than in the summer.

Oncophanes americanus

This species was present in samples taken from June to September. Because it was not collected in Woodland Washington, (the only location sampled at other times of the year), its annual life cycle is unknown.

O. americanus displayed a tendency to enter diapause when collected in late August and September. Fifty percent of the 18 larvae collected in September ceased development, although this may be due to the reversal of diapause induction by rearing conditions in the laboratory (20°C and L:D 16:8). Morphogenesis ceased after cocoon formation, at what appeared to be mature larvae. A few specimens placed at 6°C and total darkness for three months successfully completed development afterwards.

Enytus eureka

Rearing records from Spring and late Fall provide strong evidence that E. eureka can overwinter inside orange tortrix larvae (Appendix 5a,b). Oviposition occurs as late as November as was observed for recently hatched orange tortrix larvae collected at the OSU Entomology farm November 26, 1981. This species could be reared at any time of the year from the orange tortrix, but was too infrequently collected to determine any particular season of greatest abundance.

Diadegma spp.

It appears that Diadegma spp. overwinter inside the host as young larvae and that this occurs in both A. citrana and C. rosaceana (Appendix 5a,b). It should be noted that among two different Diadegma species groups recognized by H. Townes, both tortricid species were represented as hosts. This raises the question of how overwintering in hosts displaying diapause versus hosts displaying quiescence affect the phenology of Diadegma spp. and E. eureka. A. citrana often develops to a mature larval stage by early spring, the time when second and third instar OBLR are first seen to become active. It is likely that these two species of the subfamily campopleginae will not initiate development until a certain host size threshold is reached, as shown for a related species, Hyposoter exiguae from the host Trichoplusia ni (Smilowitz and Iwantsch 1973). Spring emergence is thus expected to occur earlier from A. citrana than from OBLR for these species.

Parasitoids Reared from Other
Tortricids on Caneberries

Three species of the family Tortricidae were collected and reared in the same manner as A. citrana to determine whether these species serve as alternative hosts of orange tortrix parasitoids. Non-tortricid lepidopteran larvae were seldom encountered, and therefore were not reared because of the unlikelyhood of their being important hosts of tortricid parasitoids in caneberry plantings.

Records on parasitization of the three species of the family Tortricidae will be discussed individually.

The Obliquebanded Leafroller

Special emphasis was placed on rearing Choristoneura rosaceana (Harris); (referred to as OBLR), because it is abundant and can be a pest in caneberries (Schuh and Mote 1948). Of 241 OBLR larvae reared, 26.6% were parasitized by at least 13 species (Table 9). Seven of these were also reared from the orange tortrix. Four of the six most abundant orange tortrix species were also of the greatest abundance on OBLR, accounting for 61% of total parasitism. These were Diadegma spp., Meteorus argyrotaeniae, Oncophanes americanus, and Enytus eureka. From their absence it is likely that OBLR is an unsuitable host for two other common orange tortrix parasitoids, Apanteles aristoteliae and Phytodietus vulgaris. M. argyrotaeniae was never reared from OBLR unless the orange tortrix was also present in a sample. It appears possible then that the presence of the orange tortrix influences whether M. argyrotaeniae parasitizes OBLR. Oncophanes americanus, in contrast, could be found on OBLR regardless of the presence of the orange tortrix. OBLR could be of significant benefit as an alternate host of O. americanus and other species at times when suitable orange tortrix larvae are not available. This species plus the tachinid Psuedoperichaeta erecta were 2 of the 3 most abundant parasitoids surveyed by Schuh and Mote (1948). Six of the remaining species reared from OBLR in this study are not known to be parasitoids of the orange tortrix.

Table 9. Parasitization record for Choristoneura rosaceana collected in Rubus spp., Willamette Valley, OR, 1980-1981.

Species	Determined by:	Also reared from <u>Argyrotaenia</u> <u>citrana</u>	Host instar(s) collected from:	Number reared	Percent
<u>Larval Parasitoids</u>					
<u>Diadegma</u> spp.	H. Townes	Yes	II-V	14	5.8
* <u>Meteorus</u> <u>argyrotaeniae</u> Johanson	P. Marsh	Yes	II-IV	9	3.7
<u>Oncophanes</u> <u>americanus</u> (Weed)	P. Marsh	Yes	II-VI	9	3.7
<u>Enytus</u> <u>eureka</u> (Ashmead)	L. Coop	Yes	II-IV	7	2.9
<u>Glypta</u> sp.	H. Townes	No	III-IV	6	2.5
<u>Macrocentrus</u> <u>iridescens</u> French	P. Marsh	No	III-V	3	1.2
<u>Apanteles</u> sp.	P. Marsh	No	II	3	1.2
<u>Pseudoperichaeta</u> <u>erecta</u> (Coquillett)	D. Wilder	Yes	IV-VI	3	1.2
<u>Elachertus</u> sp.	P. Hanson	Yes	II	2	0.83
<u>Microgaster</u> <u>epigoes</u> Gahan	P. Marsh	No	IV	2	0.83
* <u>Charmon</u> <u>extensor</u> (Linnaeus)	P. Marsh	No	IV	1	0.41
* <u>Meteorus</u> <u>dimidiatus</u> (Cresson)	L. Coop	Yes	V	1	0.41
<u>Bracon</u> sp.	P. Marsh	No	VI	1	0.41
Unknown spp.	--		--	3	1.2
Total parasitized				64	26.6
Non-parasitized larvae reared				177	
Total				241	
<u>Pupal Parasitoids</u>					
<u>Itopectis</u> <u>viduata</u> (Gravenhorst)	L. Coop	No	--	1	
<u>Brachymeria</u> <u>ovata</u> (Say)	E. E. Grissell	No	--	1	

* New host record

Neither of the 2 generalist pupal parasitoids reared from OBLR, Itopectis viduata and Brachymeria ovata are known to attack the orange tortrix, presumably because of a minimum size requirement for oviposition. Itopectis quadricingulata, also a generalist, is known from both species as well as Archips rosanus and Cnephasia longana.

The Omnivorous Leaf-tier

Of 34 Cnephasia longana (Haworth) larvae reared from six collections made from four locations, 21 parasitoids of five different species were reared (Table 10). All five were among the six parasitoid species most often reared from the orange tortrix.

Meteorus argyrotaeniae, one of the two most important orange tortrix parasitoids in this study, emerged from about one of every three leaf-tier larvae reared. Apanteles aristoteliae was absent from these rearings. In a study of parasitism of C. longana conducted on vetch, Vicia villosa, E. eureka was the most abundant species reared, although an average parasitism rate of only 17.4% was observed (Poonyathawan 1968). In this study 8.8% of the C. longana yielded E. eureka.

In general both the composition and abundance of larval parasitoid fauna appear similar for C. longana and A. citrana in caneberries, although this conclusion is based on a rather small number of rearings.

Of 14 parasitoid species introduced in western Oregon from 1951 to 1954 in an attempted biological control effort against C. longana,

Table 10. Parasitization record for Cnephasia longana collected in Rubus., Willamette Valley, OR 1980-1981.

Species	Determined by:	Also reared from <u>Argyrotaenia citrana</u>	Number reared:	Percent
<u>*Meteorus argyrotaeniae</u> Johanson	P. Marsh	Yes	11	32.4
<u>Diadegma</u> spp.	H. Townes	Yes	4	11.8
<u>Enytus eureka</u> (Ashmead)	L. Coop	Yes	3	8.8
<u>*Phytodietus vulgaris</u> (Cresson)	C. Loan	Yes	1	2.9
<u>Oncophanes americanus</u> (Weed)	P. Marsh	Yes	1	2.9
Unknown sp.	--		<u>1</u>	<u>1.9</u>
Total parasitized			21	61.8
Non-parasitized larvae reared			<u>13</u>	
Total			34	

* New host record

none were reared in this study. This concurs with the findings of Poonyathawan (1968) and earlier workers that no successful establishments were made.

Archips rosanus

Archips rosanus (L.) apparently rarely occurs or is relatively unnoticed in caneberries and is more often found on filbert, Corylus avellana which is grown throughout the Willamette Valley of Oregon. Four parasitoid species were reared from the eight larvae collected. Two of them, M. argyrotaenia and Meloboris sp., were also orange tortrix parasitoids in this study. The other two, Microgaster epigoges Gahan and Glypta sp. were also reared from OBLR. Comparison of other parasitoid rearing records indicate that A. rosanus has more species in common with OBLR than with the orange tortrix (Table 11).

General Discussion

A summary of alternate hosts for some common orange tortrix parasitoids resulting from this study and existing literature is given in Table 11. Only one species, Apanteles aristoteliae, appears to be specific to the orange tortrix among leafrollers collected from caneberries. This result is in agreement with other workers' observations that hosts are attacked because they are accessible within a certain habitat and are acceptable, not because they are preferred (Schwenke 1956, Townes 1969, Vinson 1976). It is likely that many of these species are native to the Pacific Northwest since none have been purposefully introduced and are relatively non-host-selective, having an average of 15 known hosts each. All of

Table 11. List of alternate hosts of some common parasitoids reared from the orange tortrix.

Parasitoid	Host species ¹				Total number hosts recorded
	Orange tortrix	Obliquebanded leafroller	Omnivorous leaf-tier	<u>Archips rosanus</u>	
Braconidae					
<u>Oncophanes americanus</u> (weed)	x ^{ac}	x ^{abe}	x ^a		20
<u>Apanteles aristoteliae</u> vier.	x ^{abcd}				8
<u>Meteorus argyrotaenia</u> Johan.	x ^{abc}	x ^a	x ^a	x ^a	9
<u>Bracon gelechia</u> (Ash.)	x ^b		x ^f		34
Ichneumonidae					
<u>Enytus eureka</u> (Ash.)	x ^{acd}	x ^{abe}	x ^{abf}		9
<u>Diadegma interruptum pterophorae</u> (Ash.)	x ^{abc}	x ^{abe}	x ^{ab}	x ^{ab}	9
<u>Itopectis quadricingulata</u> (Prov.)	x ^{ad}	x ^{be}	x ^b	x ^{bg}	28
<u>Ischnus inquisitorious atricollaris</u> (Walsh)	x ^c	x ^{be}	x ^f	x ^g	7
<u>Phytodietus vulgaris</u> Cress.	x ^{ac}		x ^a		4
Tachinidae					
<u>Pseudoperichaeta erecta</u> (Coq.)	x ^{ah}	x ^{ahe}		x ^h	27

¹ Source; host plant(s):

a Current research data, 1980-1981; Rubus spp.

b Krombein et al., 1979.

c Johansen & Breakey, 1949; Breakey, 1951; Rubus ideaus.

d Rosenstiel, 1949; Rubus ideaus.

e Schuh & Mote, 1948; Rubus ideaus.

f Poonyathawon, 1968; various hosts not including Rubus spp.

g Aliniaze, 1977; Corylus avellana (filbert).

h Arnaud, 1978.

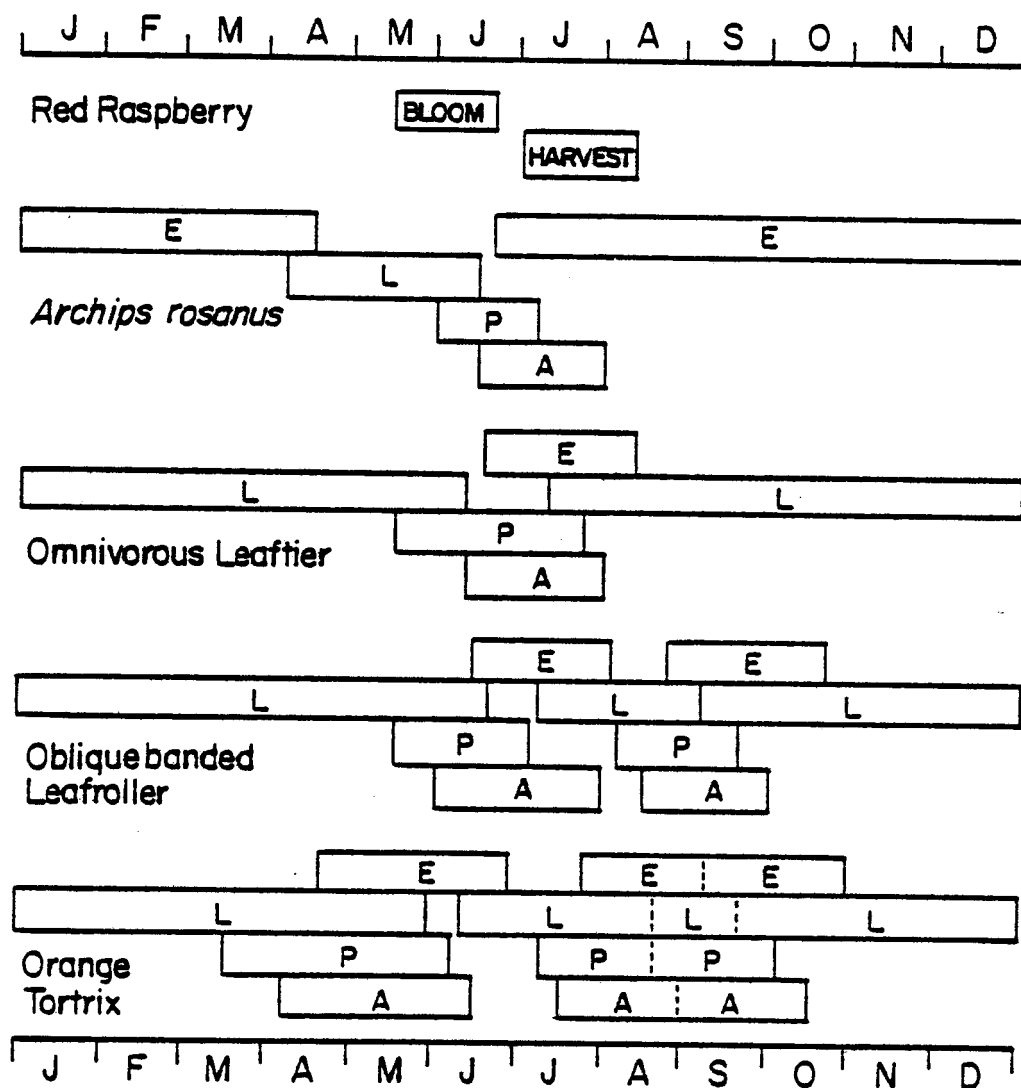


Figure 3. Seasonal representation of red raspberry bloom and harvest and life stages of four tortricid species in western Oregon.

the six most abundant species reared from A. citrana appear to be multivoltine and few, if any, appear synchronized to a particular host species.

Sympatry of alternate hosts with the orange tortrix may profoundly influence the latter's regulation. Although the possibility exists that alternate hosts may serve as "competitors" for host-seeking parasitoids, their widely differing seasonal life cycles may add the stabilizing element of a more constant supply of hosts. Both C. longana and A. rosanus are univoltine and approach larval maturity by early June, when orange tortrix populations have usually pupated or emerged (Figure 3). The overwintering generation of OBLR follows a similar course. Therefore the presence of all three species may reduce potential for parasite emigration, thus allowing local parasitoid populations to increase despite reduced numbers of the orange tortrix.

The two univoltine species are not significant contaminants in red raspberries, because they are not present as larvae during harvest. The first generation of the OBLR may pose a contamination problem in berries during the latter portion of harvest and on later-developed Rubus spp. All four tortricids are polyphagous (Powell 1964), which heightens the complexities involved with habitats surrounding caneberries, alternate hosts, and dispersal abilities in the regulation of the orange tortrix by parasitoids.

LABORATORY STUDIES

Adult Longevity

Results expressed as mean and maximum adult life for four common parasitoids are given in Table 12. Females within each species lived longer than is required for egg to adult development at 20°C. This suggests that generations greatly overlap in the field. There appears to be a relationship between longevity and size. All braconid species were shorter lived than the mean of 60 and 27 days seen for the larger Phytodietus vulgaris females and males, respectively. Females of the smallest species studied, Oncophanes americanus, lived an average of only 20.4 days.

The two smaller ichneumonids Enytus eureka and Diadegma spp. usually did not live more than a week under the conditions provided. However one Diadegma spp. female survived 43 days. The inability to rear these species in the laboratory during this study was probably due to their short lifespan.

Laboratory Rearing

Of the six species of parasitoids for which laboratory rearing was attempted, three were found to be quite easily reared under the conditions provided of screened cages, honey and water, and artificial diet-reared orange tortrix hosts. These were Oncophanes americanus, Phytodietus vulgaris, and Apanteles aristoteliae. The latter two were reared extensively for additional studies. All three species exhibited arrhenotoky, and were able to mate and produce progeny of both sexes at approximately even sex ratios.

Table 12. Adult longevity of four orange tortrix parasitoids; $21 \pm 1.5^\circ\text{C}$, $60 \pm 15\%$ R.H.

Species	Sex	N	Longevity (Days)	
			$\bar{X} \pm \text{SD}$	Max
<u>Apanteles</u>				
<u>aristoteliae</u>	♀	10	44.0 ± 7.4	55
	♂	7	21.3 ± 5.3	33
<u>Meteorus</u>				
<u>argyrotaeniae</u>	♀	17	48.8 ± 14.4	69
<u>Oncophanes</u>				
<u>americanus</u>	♀	8	20.4 ± 4.5	28
<u>Phytodietus</u>				
<u>vulgaris</u>	♀	10	60.0 ± 9.57	74
	♂	10	27.3 ± 8.51	43

Enytus eureka and Diadegma spp. could not be reared in the laboratory. Because of an apparent inhibiting effect of the artificial diet on oviposition, M. argyrotaeniae females were provided with orange tortrix larvae rolled within terminal red raspberry leaves. Parasitization was successful using this technique, indicating that this species may depend on some characteristic(s) of the host plant for oviposition initiation. However, it was not determined if host acceptance was dependant upon some chemical or physical cue of the plant. All progeny were female, which corroborates literature indicating this species is thelytokous.

The ease with which these orange tortrix parasites are reared strengthens their candidacy for further work detailing their biologies and for mass culturing for inundative or inoculative release projects.

Developmental Periods

All four parasitoids reared successfully except M. argyrotaeniae were reared for a second generation in the laboratory with no appreciable mortality. No differences in developmental periods resulted between sexes for the three arrhenotokous species, therefore these data are combined in Table 13. Egg plus larval development, either in or on the orange tortrix, ranged from an average of 7.8 days for O. americanus to 20.5 days for A. aristoteliae at 20°C. The variance associated with egg plus larval development was relatively small for each species, with no apparent effects of host size on developmental rate. This conforms with expectations of the three

Table 13. Development periods of laboratory reared parasitoids of the orange tortrix at $20 \pm 1^{\circ}\text{C}$ and LD 16:8.

Species	N	Developmental interval (days)			
		egg to cocoon	cocoon to adult	egg to adult	$\bar{X} \pm \text{SD}$
		$\bar{X} \pm \text{SD}$	$\bar{X} \pm \text{SD}$	range	
<u>Oncophanes</u> <u>americanus</u>	19	7.8 ± 0.69	10.3 ± 0.45	17-21	18.1 ± 0.88
<u>Meteorus</u> <u>argyrotaeniae</u>	13	12.2 ± 1.07	9.2 ± 0.55	19-23	21.3 ± 1.11
<u>Phytodietus</u> <u>vulgaris</u>	34	15.1 ± 1.66	11.9 ± 0.88	23-32	26.9 ± 1.90
<u>Apanteles</u> <u>aristoteliae</u>	22	20.5 ± 1.85	12.2 ± 0.69	30-36	32.7 ± 1.70

species which attack large host larvae. A. aristoteliae attacks small to large sized hosts however, which might lead to the suspicion that parasitoid development is suppressed in small hosts. Only an occasional tendency for this was seen, however. The parasitoid was able to develop in second instar hosts at the same rate as in fourth and fifth instar hosts in this study.

The period from cocoon formation to emergence, which includes the prepupal and pupal stages, averaged 9.2 to 12.2 days for the four species. The variance associated with this interval was even less than was observed for egg plus larval development in each case, and would probably be even less had observations been made more frequently than once a day. Both of the two most common campoplegine ichneumonids from field collected hosts, E. eureka and Diadegma spp., only spent an average of 8.2 days inside cocoons. Although it was initially hoped that the egg plus larval developmental intervals could be estimated from field collected hosts for these two species, such factors as host size and time of year probably contributed to the large range in values obtained. It can be approximated that egg plus larval development requires 11-17 days for each of these species.

Total development time from egg to adult ranged from 18.1 to 32.7 days for the four species reared. These are all of shorter duration than the 49 days required for orange tortrix egg to adult development at 20°C (estimated from Basinger 1938). Knowledge of development periods at a constant temperature was useful in this study for evaluating parasitoid host size relationships and for making

conclusions on seasonality. Additionally, this information could be used in conjunction either with adult longevity in making rough estimates on voltinism, or with fecundity estimates for determining intrinsic rates of increase (r_m).

Apanteles aristoteliae; Development at Different Temperatures

The durations of egg plus larval and pupal stages at various temperatures are given in Table 14. Developmental time from egg to adult ranged from 20.3 days at 28°C to 114.3 days at 12.0°C. Survival was nearly 100% at all temperatures except 32°C at which none survived. This temperature is known to be higher than the upper developmental threshold of orange tortrix larvae (Basinger 1938, Kido et al. 1981). Host larvae were observed to do little or no feeding and did not molt at this temperature although some survived for up to a month. At 28°C, rate of development began to level off for the egg plus larval stages, but not the pupal stage. This may indicate that the latter has a higher upper development threshold. The test for this could be to place A. aristoteliae at 30-32°C immediately after cocoon formation from a lower temperature. Regression equations for daily percent development using either all five temperatures at which successful development occurred, or with only the lowest four temperatures appear in Table 15. Since egg plus larval development is most linearly represented by only the four lowest temperatures, thermal constants estimated by this range may be more accurate, whereas thermal constants representing pupal development were relatively the same for either temperature range used.

Table 14. Duration of developmental stages (days) of Apanteles aristoteliae as related to temperature.

Temp. °C	N	<u>Egg plus larval stage</u>	<u>Pupal stage</u>	<u>Egg to adult</u>
		$\bar{X} \pm SD$	$\bar{X} \pm SD$	$\bar{X} \pm SD$
12.0	16	67.9 \pm 5.26	46.4 \pm 6.02	114.3 \pm 8.80
16.7	36	31.6 \pm 3.95	18.9 \pm 0.90	49.9 \pm 4.98
20.0	22	20.5 \pm 1.85	12.2 \pm 0.69	32.7 \pm 1.70
24.0	22	14.5 \pm 1.26	7.9 \pm 0.47	22.3 \pm 1.32
28.0	24	13.9 \pm 2.00	6.3 \pm 0.48	20.3 \pm 2.23

Table 15. Regression equations and thermal constants for rate of development of Apanteles aristoteliae in relation to temperature.

Stage(s)	Range of temp. (°C)	Regression equation ^a	x-intercept ^b	1/m	r ²
Egg plus larva	12.0-28.0	$\hat{y}=0.0039x-0.0303$	7.9	259.8	.96
	12.0-24.0	$\hat{y}=0.0046x-0.0419$	9.2	212.3	.99
Pupa	12.0-28.0	$\hat{y}=0.0088x-0.0891$	10.1	113.5	.99
	12.0-24.0	$\hat{y}=0.0088x-0.0882$	10.1	114.3	.98
Egg to adult	12.0-28.0	$\hat{y}=0.0026x-0.0235$	8.7	371.6	.98
	12.0-24.0	$\hat{y}=0.0030x-0.0286$	9.5	332.6	.99

^a Regression equation is $\hat{y} = mx + b$ where \hat{y} is proportion of development per day and x is temp. in °C.

^b x-intercept and 1/m are estimates of threshold temperatures and thermal requirements, respectively.

The low temperature thresholds derived are 9.2°C for egg plus larval development and 10.1°C for pupal development. Thermal requirements for development, calculated using the respective threshold estimates were: egg plus larva; 218.9 degree days, and pupa; 114.3 degree days. The calculated thermal constants for egg to adult development were: threshold temperature; 9.5°C, and thermal requirement; 332.6 degree days.

It appears that this parasitoid has a significantly higher threshold temperature than does the orange tortrix, which was estimated to be near 5°C (Appendix 1). At the lowest temperature measured, 12°C, a suppression of host development was apparently occurring, since egg plus larval development required a mean of 68 days while a non-parasitized host required an estimated 55-60 days larval development. At higher temperatures, A. aristoteliae formed its cocoon at around the same time that unparasitized orange tortrix pupate.

Using these estimates of thermal constants for development, the PETE phenological model (Welch et al. 1978) was used to simulate the seasonal development and voltinism of A. aristoteliae. Additional parameters estimated for the simulation included; an adult activity threshold, a preoviposition interval, adult longevity, an upper developmental threshold, and a provision for developmental heterogeneity (Appendix 6). The model was calibrated with spring and partial first generation emergence records from Woodland, Washington for 1981 (Figure 4). Using Corvallis, Oregon weather data averaged

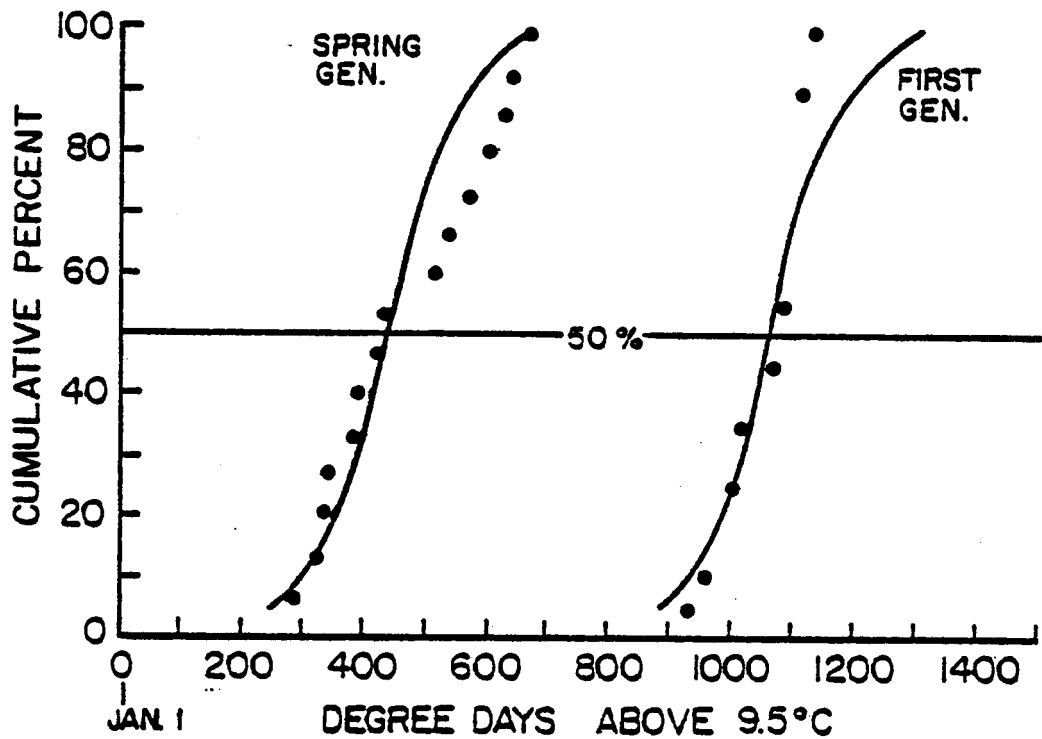


Figure 4. Cumulative emergence of *Apanteles aristoteliae* as observed from Woodland, WA. 1981 (points); and predicted by PETE phenology model (solid lines).

over the past 35 years, the model predicted dates for 50% adult emergence of successive generations on June 1, July 19, Aug. 25, and Oct. 21. Thus three complete and a partial fourth generation were estimated, one full generation more than is commonly given for the orange tortrix.

Judging from the large degree of overlap observed for the host's 2-3 generations and from A. aristoteliae's extended spring emergence period observed at Woodland, Washington, this parasitoid probably also develops greatly overlapping broods as well.

This might be viewed as a means of synchronization of an orange tortrix parasitoid which approaches a high level of host specificity. Since A. aristoteliae appears to have no alternate hosts in caneberries, emigration must occur when orange tortrix larvae are not present. Thus heterogeneity in development plus the observed ability to attack a wide range of host sizes would be adaptive for remaining with local host populations. This may serve to avoid risks associated with emigration to a new local exploited by the host. Consistency of parasitization records of A. aristoteliae on a wide variety of host crops throughout A. citrana's range, plus the relatively small list of alternate hosts indicate that this species is well adapted to A. citrana.

Phytodietus vulgaris; Life History and Diapause Characteristics

Phytodietus vulgaris, a common external parasitoid of the orange tortrix, is placed in the subfamily Tryphoninae, family Ichneumonidae. A description of the life history as well as the results of preliminary experiments on the occurrence of diapause are treated here.

Life Stages

The egg is usually oviposited on the dorsum of the meso or metanotum of its host. A stalk inserted just under the host integument securely attaches the egg and all larval stages until the host is consumed. The egg is white, ovate and shiny. It measures ca. 0.35 x 0.15 mm excluding the pedicel. The egg hatches in four to six days. This indicates that uterine egg development does not occur for this species, although it does for some others placed in the subfamily Tryphoninae (Clausen 1940).

In both field collected and laboratory reared specimens the eggs did not always hatch during this study. More often than not the host would develop into a normal adult if the egg proved inviable. Commonly two or more eggs are found per field collected larva. Females would oviposit repeatedly into the same host in the laboratory. This usually resulted in at least one egg hatching. Except for one unusual case where an orange tortrix was collected with a P. vulgaris egg at the posterior end as well as on the thorax, only one progeny per host will be produced. Additional parasitoid larvae are killed usually by the largest larva present. This often did not

occur until the middle instars were reached. Apparently the larvae develop through five larval instars. This is based on the classification of head capsule measurements (Table 16). No difference in head capsule widths between sexes was observed.

The first four instars look similar to each other except for size, and all are of the normal hymenopteriform type being essentially legless, 13-segmented with a well developed, sclerotized head. In instars one through four the head capsule is black, changing to white during the fifth. Development time at 20°C averages about 1.5 to 3.5 days for each instar, with total larval development averaging 11.3 days to the time of cocoon construction (Table 16). Each successive stadia feeds from a new position on the host. The host is apparently not greatly disturbed throughout most of the parasitoids larval development and continues to feed and molt normally. When the fifth-instar P. vulgaris reaches a size about equal to that of its host, it disengages from the pedicel and positions itself to finish consuming its host. A translucent, capsule shaped cocoon is constructed within one day after host consumption at the same site the host had occupied. Non-diapausing individuals will change form within two or three days to become more elongate with fairly well developed eyespots. This pre-pupal stage has been termed the pronymph for other Tryphoninae (Morris 1937). One day after this change the meconium is deposited in one mass at the end of the cocoon. One or two days later pupation occurs. Emergence occurs after an additional 7 or 8 days.

Adults were observed to chew an irregular opening through the end of the cocoon within a few minutes after first exposure to light upon

Table 16. Development periods of life stages of non-diapausing *Phytodietus vulgaris* at $20\pm 1^{\circ}\text{C}$ and head capsule measurements of larval instars.

Stage	Duration (days)		Headcapsule width (mm)	
	N	$\bar{X} \pm \text{SD}$	N	$\bar{X} \pm \text{SD}$
Egg	28	5.14 ± 0.71	-	-
L I	21	3.29 ± 1.27	18	0.174 ± 0.0082
L II	22	2.23 ± 0.92	21	0.266 ± 0.0158
L III	25	1.76 ± 0.66	24	0.373 ± 0.0201
L IV	29	1.59 ± 0.57	29	0.514 ± 0.0191
L V-cocoon formation	30	2.40 ± 0.56	19	0.678 ± 0.0665
Cocoon formation-pupa	22	4.55 ± 0.86	-	-
Pupa to emergence	22	7.32 ± 0.72	-	-
Egg to emergence	26	28.19 ± 2.79	-	-

completion of development. Total development time from egg to adult averaged 26.9 days when diapause did not occur. No differences in developmental times between sexes were found for any stage.

Adult Activity

Mating activity was observed immediately after emergence. Males mated more than once and the mating of siblings was observed. Females were observed ovipositing within three or four days after emergence, and mating was not required for oviposition. During host location, antennalation was greatly excited when host silk or frass were encountered. The following summary was made from more than twenty-two observations on oviposition behavior.

Hosts ranging from third to sixth instars were attacked, although oviposition into small third instars usually proved unsuccessful and the largest fifth and sixth instars sometimes were not physically overcome. Usually the ovipositor was inserted just under the integument in the mid-posterior region of the host for paralyzation. Host activity was subdued within a few seconds although the ovipositor remained in place in the host for an average of 42 seconds. Next, 10 to 45 seconds were spent locating an oviposition site by probing with the ovipositor until a place just posterior to the pronotum was found. Here the ovipositor was inserted for 17 to 45 seconds while an exposed egg moved down the grooved ovipositor by a stalk which was the only part actually forced into the host integument. Additional eggs usually were oviposited at least a minute or two later, after the female had flown off and returned again. In 30 to 50 percent of the hosts, a

non-lethal host feeding period of one to two minutes was observed where either the ooze from the sting wound was embibed or one of the prolegs was chewed upon with the mandibles. About 16% of the hosts were nearly completely consumed by host feeding thus being killed, and this often included larvae too small for oviposition, as well as hosts already parasitized.

Diapause

After several P. vulgaris specimens collected in October and November of 1980 in Woodland, WA (latitude 45° 52'N.) were observed to cease development in the mature larval stage just after constructing the cocoon, attempts were made to determine the conditions responsible for initiating and terminating this arrested development. First, P. vulgaris were reared in the lab at 20°C under three photoperiodic regimes. Short days (LD 10:14) were found to induce 100% dormancy while long days (LD 14:10 and 16:8) did not. The results indicate that P. vulgaris underwent a photoperiodically induced diapause and that the critical photoperiod for diapause induction was between 10 and 14 hours light per day. Various preliminary studies on the termination of this condition (Table 17), indicated that: 1) Long daylengths at 20°C were responsible for diapause termination. 2) No prolonged exposure to either cool temperatures or short daylengths was required for termination. 3) The critical photoperiod for termination in the laboratory was probably between LD 13:11 and 14:10

Table 17. Summary of preliminary experiments on diapause termination of Phytodietus vulgaris.

<u>Previous conditions^a</u>		<u>New conditions</u>		N	Percent terminating diapause	Interval to pupation; $\bar{x} \pm \text{SD}; \text{days}$
Temp. °C.	Photoperiod hr. L:D	Temp. °C.	Photoperiod hr. L:D			
20 ⁰	10:14	20 ⁰	16:8	13	100%	12.2 \pm 3.93
20 ⁰	10:14	20 ⁰	14:10	5	100%	12.8 \pm 2.17
20 ⁰	10:14	6 ⁰	14:10	5	0%	-
11 ⁰	10:14	20 ⁰	16:8	14	100%	10.3 \pm 1.28
11 ⁰	10:14	20 ⁰	10:14	11	0%	-
6 ⁰	10:14	20 ⁰	13.5:10.5	5	20%	-
6 ⁰	10:14	20 ⁰	13.0:11.0	9	0%	-
6 ⁰	10:14	20 ⁰	12.5:11.5	7	0%	-
6 ⁰	14:10	20 ⁰	16:8	10	100%	10.7 \pm 4.37
6 ⁰	14:10	20 ⁰	10:14	3	0%	-

^aMaintaining diapause for at least two weeks.

at 20°C. At a low temperature of 6°C and photoperiod of LD 14:10 diapause was maintained, although this was perhaps because the temperature was below the threshold for development.

The interval to pupation following transition from diapause maintaining to terminating conditions differed slightly but not significantly between the temperatures 6, 11, and 20°C (Table 17), indicating that temperature may have had little effect upon diapause development. An overall average time for the transition to pupation interval of 11.5 days was obtained for the four cases in which diapause was terminated. This is six days longer than was required for non-diapausing P. vulgaris to pass from cocoon formation to pupae. It can be interpreted that at 20°C diapause was terminated within six days and normal development had resumed. This is assuming that no morphogenesis occurred between cocoon formation and the onset of diapause and during the diapausing period. A single P. vulgaris cocoon collected in the field on March 2, 1981 had apparently terminated diapause and resumed development because it pupated only three days later at 20°C and LD 16:8. If diapause were maintained up to the time of collection this interval would have been expected to be 11.5 days as the results noted in laboratory studies would suggest. Two additional experiments were conducted to determine which stages of development are sensitive to short days for diapause induction. First an examination of the effects of transferring different stages of P. vulgaris from long to short day conditions was conducted. Larvae transferred through the third instar all diapaused. When fourth

instars were transferred from long to short days, 48% diapaused, while none diapaused when transferred while in the fifth instar (Figure 5).

The result may suggest that only the fourth and fifth instars are sensitive to photoperiod for determination of diapause or at least that they are able to reverse any effects of daylength on earlier stages. The photoperiod counter may provide an alternative explanation in which certain numbers of long and/or short-day cycles during the stages sensitive to photoperiod are required for diapause induction (Saunders, 1976).

The reciprocal experiment of transferring different stages of P. vulgaris from short to long day conditions was conducted. Because the condition of arrested development is reversible by long days, the criterion for detection of diapause used was the interval between cocoon formation and pupation. Results are presented in Table 18. No evidence of diapause was seen until P. vulgaris was transferred from short to long days at the fifth instar, for which a slightly greater interval for cocoon formation to pupation was required. Larvae transferred on the day of cocoon formation required a mean of 3.1 days more to pupate. This indicates a brief suppression of development. When transfer was made the day following cocoon formation, the average interval to pupation increased by two more days. This trend suggests that diapause intensity increased through this time or the incidence of diapause was increased. Average days to pupation from time of transfer at one, two and four days after cocoon formation were not significantly different from those transferred at longer intervals

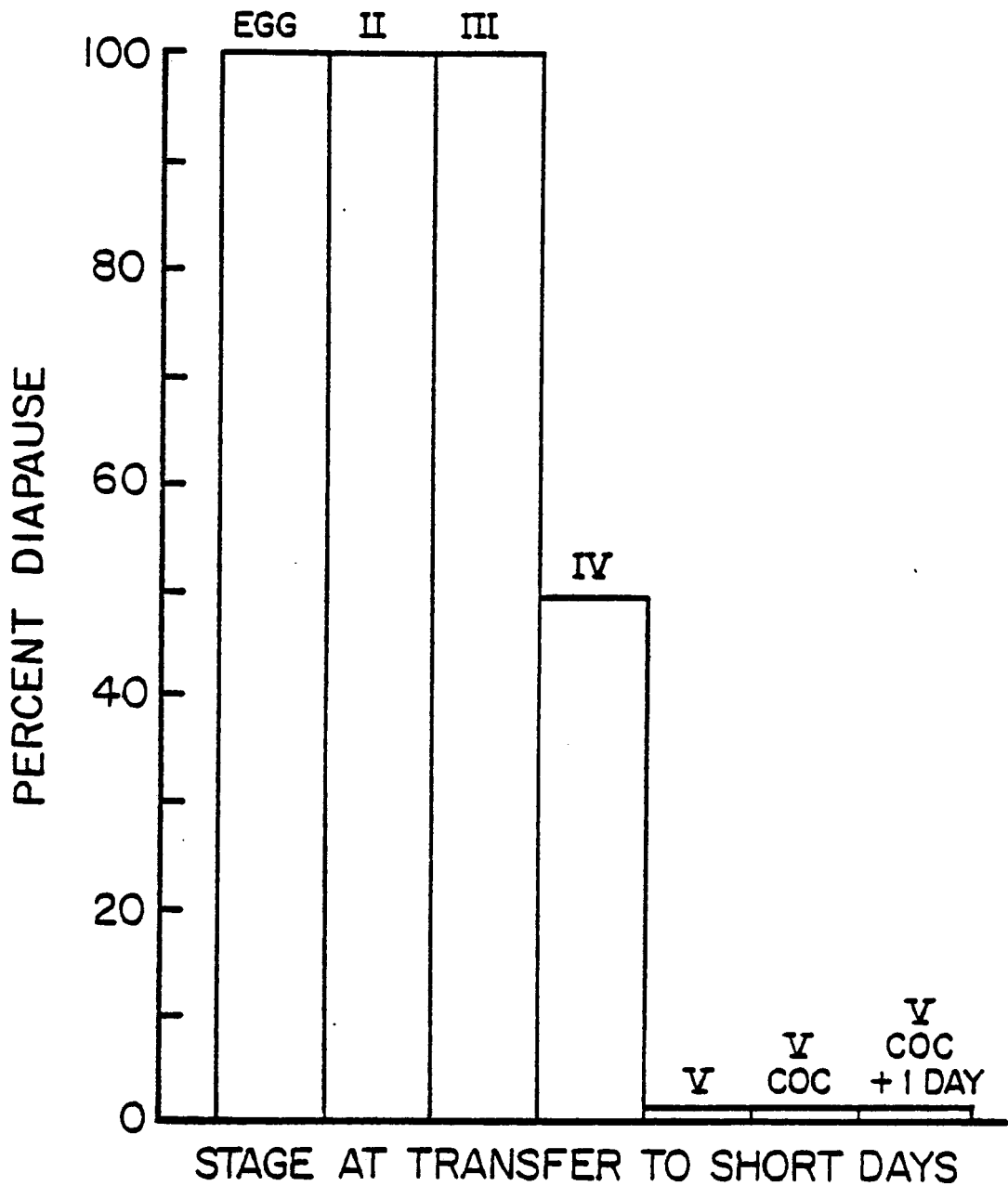


Figure 5. Percent diapause obtained for different larval stages of *Phytodietus vulgaris* transferred from long days (LD 16:8) to short days (LD 10:14) at 20°C.

Table 18. Effects of transferring different developmental stages of *Phytodietus vulgaris* from short to long day photoperiods; measured as interval to pupation, $20 \pm 1^\circ\text{C}$.

Stage of transfer 10:14 to 16:8 L:D	Interval; date of cocoon formation to pupa, days ⁴			Interval; date of transfer to pupa, days ⁴	
	N	Range	$\bar{X} \pm \text{SD}$	Range	$\bar{X} \pm \text{SD}$
Control ¹	22	3-7	4.5 ± 0.86^a	-	-
L III	2	4-5	$4.5 \pm 0.71^*$	-	-
L IV	10	4-6	4.9 ± 0.74^{ab}	-	-
L V	4	5-7	6.0 ± 1.15^b	-	-
L V coc. ²	4	6-10	8.0 ± 1.63^c	6-10	8.0 ± 1.63^a
L V coc + 1 day	4	-	-	7-12	10.0 ± 2.16^{ab}
L V coc. + 2 days	5	-	-	10-14	12.4 ± 1.52^b
L V coc. + 4 days	5	-	-	12-16	12.2 ± 1.79^b
L V in diapause ³	18	-	-	9-15	11.7 ± 2.14^b

¹ Long day conditions throughout development.

² Date cocoon formed, normally 2 or 3 days after molt to LV.

³ Diapause maintained for a variable period exceeding 2 weeks.

⁴ Means in same column followed by same letters are not significantly different ($p < 0.01$, LSD test).

* Not included in analysis because of small sample size.

following cocoon formation. This supports preliminary observations that in the laboratory a certain number of long days is required to terminate diapause regardless of exposure to sustained cold temperatures or short day photoperiods. A few species which did not require chilling have been shown to end diapause in response to daylengths in nature, including Wyeomia smithii (Smith and Brust 1971) and Meleoma signoretti (Tauber and Tauber 1976). In others which are also known to terminate diapause in response to photoperiod in the laboratory, however, termination of diapause in the field occurs long before natural daylengths have reached the intervals found for termination in the laboratory. These include Chrysopa carnea (Tauber and Tauber (1973) and Ostrinia nubilalis (McLeod and Beck (1963). Tauber and Tauber (1976) advised that in cases where no chilling was required in photoperiodically terminated diapause in the laboratory, that long daylengths probably end diapause in nature as well. Therefore, it is reasonable to conclude that photoperiod is the principle stimulus for diapause termination with P. vulgaris. Another ichneumonid, Pimpla instigator F., was also shown to terminate diapause at any time in the laboratory by exposure to long-day photoperiods. No evidence on the influence of daylengths in nature was presented, however (Claret 1973).

CONCLUSION

The practice of machine harvesting and in some cases, hand harvesting have usually relied upon a single "clean up" insecticide application prior to harvest to prevent contamination of fruit by arthropods residing in caneberries, most notably lepidopteran larvae, root weevils, spiders and ladybird beetles (Kieffer 1979). Normally, orange tortrix populations exist at endemic and almost undetectable levels in caneberries. However, a high fecundity, several generations per year, and an abundant food supply can lead to potentially explosive outbreaks when natural enemies are absent.

This research has identified several parasitoids which cause mortality to A. citrana in stages relatively invulnerable to predators and insecticides: larger larvae and pupae. Three species in particular are considered to be of greatest value in providing natural control. These are Apanteles aristoteliae, Meteorus argyrotaeniae, and Oncophanes americanus. The preliminary efforts made in clarifying the life history and alternate hosts of these and other species will be of value in the development of integrated control of the orange tortrix. Recognition of the effects of cultural practices and insecticide applications on the performance of these natural enemies appears highly warranted.

SUMMARY

A parasitoid survey was conducted on populations of the orange tortrix, Argyrotaenia citrana at a number of locations in the

Willamette Valley, Oregon where Rubus spp. are grown commercially. Of more than 1400 larvae reared, 14 species contributed to a total apparant parasitism of 34.0%. Sixty three percent of the parasitism was due to two braconids, Apanteles aristoteliae and Meteorus argyrotaeniae. These species were common at all locations sampled. Another 30% of total parasitism was attributed to three ichneumonids; Phytodietus vulgaris, Enytus eureka, Diadegma spp., and one braconid; Oncophanes americanus.

All six species have been reported previously as parasitizing the orange tortrix on Rubus spp. in the Pacific Northwest. Two additional species, Parania geniculata and Meteorus dimidiatus, which represent new host-parasite records contributed 4.5% of total parasitism. The hyperparasitoid species, Stictopisthus sp. and Spilochalcis sp. comprised only 1.1% of total larval parasitism. Of four parasitoid species reared from the 27 pupae also collected, Itoplectis quadricingulata was the most abundant.

O. americanus was nearly as abundant, if present in a sample, as were A. aristoteliae and M. argyrotaeniae. P. vulgaris and E. eureka were widespread but were not particularly abundant, indicating that they may be of a relatively lesser importance.

Host sizes collected and exited from as measured by head capsule measurements were compared for major contributing species. Apparent host sizes attacked were also evaluated with the aid of laboratory rearing observations. Although different species in the complex could vary greatly as to size of host larva attacked, in nearly all

instances fourth instars or larger were exited from. When host density is used as a criterion for separating results into two categories, fourth instar parasitism was 73.0% versus 26.1% for low versus high density infestations. These results suggest that parasitoids may be a factor important in maintaining A. citrana at endemic levels. Excessive or improperly timed insecticide applications may have been involved, since the two fields with high density populations had been sprayed at least twice during this study.

Of the six most abundant species, all could be collected from the field at most times during the year. Parasitism was greatest during the summer. M. argyrotaeniae was mainly collected during the summer, while A. aristoteliae was important in fall and summer months. P. vulgaris was more abundant during the fall.

Four parasitoid species were indicated to overwinter inside their hosts while two diapause inside cocoons.

Four of the six most abundant orange tortrix parasitoids were also most often reared from another common tortricid on Rubus spp., Choristoneura rosaceana (Harris). Five of the six were also reared from Cnephasia longana (Haw). Only Apanteles aristoteliae appears to lack other tortricid hosts in caneberries, indicating that it is relatively host specialized. With this exception, then, populations of other tortricids in Rubus may affect parasitization rates of the orange tortrix. All leafroller moths and most major parasitoids studied appear to be relatively polyphagous, implicating a high degree of interaction with other habitats surrounding caneberry fields.

In studies conducted in the laboratory, female adult longevity for four species parasitoid roughly corresponded with size, ranging from a mean of 20.4 days for Oncophanes americanus to 60.0 days for Phytodietus vulgaris. Males lived a much shorter length of time than did females. Four species were successfully reared in the laboratory, but among these M. argyrotaeniae required hosts contained in live plant material rather than hosts accompanied with an artificial diet. Developmental times at 20°C from egg to adult ranged from 18.1 days for Oncophanes americanus to 32.7 days for Apanteles aristoteliae. These intervals were all shorter than is known for larval development of the orange tortrix.

Apanteles aristoteliae was successfully reared at the temperatures 12.0, 16.7, 20.0, 24.0, and 28.0°C. Host mortality occurred at 30.0°C, preventing parasitoid egg-larval development. Thermal constants for egg-to-adult development calculated by linear regression were: threshold temperature; 9.5°C, and thermal requirement; 332.6 degree-days. Three to four generations per year were estimated by the PETE phenology model, using adult emergence calibrated to field data for 1981 in Woodland, Washington. Of the overwintering and first generations, 50% adult emergence occurred on June 1 and July 19, indicating a shorter generation time than occurs for the orange tortrix.

Phytodietus vulgaris, an ectoparasitic ichneumonid, had five larval instars and displayed photoperiodically induced and terminated diapause in the laboratory. Sensitivity to photoperiod occurred

throughout the fourth and fifth instars, and mature larvae remained sensitive for diapause maintenance, i.e.; there was no chilling requirement for diapause termination. The critical photoperiod for diapause induction was between LD 10:14 and 14:10, and for termination between LD 13:11 and 14:10 at 20°C.

IV. ORANGE TORTRIX OVIPOSITION AND EGG DEVELOPMENT

INTRODUCTION

Control of the orange tortrix has traditionally been directed at the larval stage in red raspberries. Currently, if additional control is sought beyond that expected during the preharvest treatment, an insecticide is usually applied just prior to bloom. However, contamination during harvest may still occur when using a prebloom spray, perhaps because nearly all of the overwintering population are by then at a later, less susceptible, stage of development. Young larval stages of the first generation are difficult to detect. During bloom, when they usually first appear, the choice of insecticides is limited to those believed to be of a lower efficacy in order to protect the pollinators. A model predicting the presence of early larval stages would be desirable to aid in the selection and proper timing of control measures of this insect.

Beyond simply detecting the presence or absence of a population, pheromone traps are becoming widely used in conjunction with temperature driven physiological time models for aiding in timing of insecticide applications. Pheromone traps have proven to be highly effective in detecting first emergence of other tortricid species (Riedl et al. 1976, Baker et al. 1980). For prediction of first oviposition, additional data are required on possible emergence differences between sexes, intervals required for mating and preoviposition, and oviposition behavior. The subsequent prediction

of first egg hatch requires, using the method of degree day summation, that the low temperature threshold and heat units for development (thermal constants) of the egg stage be determined. In order to substantiate and add to laboratory results obtained by Basinger (1938), the present work emphasizes orange tortrix oviposition and egg development in the field. The objectives of this study were: 1) to estimate the interval required for mating and oviposition by orange tortrix under semi-natural (caged) conditions; 2) to estimate the thermal constants needed to predict egg hatch from laboratory as well as field embryonic development data; 3) to compare three commonly used methods of summing degree-days for their accuracy in predicting egg hatch; and 4) to examine other available data such as spring emergence patterns that may affect interpretation of pheromone trap catches.

MATERIALS AND METHODS

Oviposition Behavior

On July 13, Sept. 10, and Oct. 9, 1981; 10, 7, and 7 pairs of F₁ orange tortrix adults were placed in a 1.83 m³ screened cage covering 10-15 red raspberry primocanes. All other plant material and debris had been removed to reduce alternative oviposition sites. All leaves on each cane were carefully inspected daily for egg masses. Conduit pipes which provided the internal structural support for the cages were also inspected because oviposition occasionally occurred there. Dates and exact positions were tagged at each location where

egg masses were found. The number of eggs per egg mass were counted using a dissecting microscope in the laboratory.

Egg Development at Constant Temperatures

Orange tortrix egg masses were obtained by placing wax paper of dimensions ca. 10x15 cm overnight in a 20x20x40 cm screened cage containing orange tortrix adults reared in the laboratory from field collected larvae. The following morning egg masses were placed individually in 22 ml plastic cups with paper lids. The cups were randomized and 8 to 15 were placed in plastic containers partially filled with a 19.9 wt.% solution of potassium hydroxide which maintains a relative humidity of $78 \pm 1\%$ over the range of temperatures used in this study (Solomon 1951). The plastic containers were kept at 12.0, 16.0, 20.0, 24.0, 28.0, and $32.0 \pm 1.0^{\circ}\text{C}$. in Percival® incubators. Egg masses were observed daily as eclosion approached. Dates and approximate times of 50% hatch were recorded for each egg mass as well as the total percent hatch.

Linear regression was used to estimate a developmental threshold temperature and thermal unit requirement for 50% hatch. These results were compared to those calculated from Basinger (1938) by analysis of variance (Neter and Wasserman 1974).

Egg Development Under Field Conditions

On May 27, July 17, September 14, and October 12, newly deposited egg masses on red raspberry leaves in field cages were tagged. On June 28, and July 17, eggs were obtained from caged adults in the laboratory, placed in 29 ml plastic cups with paper lids, inside the same Stevenson screen (weather shelter) used to house the hygrothermograph¹ for recording temperature data during this study. From 6 to 9 egg masses held under these conditions were checked at least daily for eclosion. Date of 50% hatch, number of eggs and percent hatch were recorded for each egg mass.

Estimation of Thermal Constants

Estimates of the developmental threshold temperature and thermal requirement for orange tortrix egg development were determined in the following manner. Six threshold temperatures were tested in accumulating heat units for each of four egg development periods in the field. The temperature which yielded the lowest coefficient of variation calculated from degree-day totals was chosen as the threshold. The average degree-day total at that threshold was then selected as the thermal requirement.

Three different methods commonly associated with the summation of degree-days were used in order to compare their adequacy. The least

¹Weather Measure Corporation, Sacramento, California.

precise of those tested was:

$$\frac{\text{max} + \text{min} - T}{2}$$

where max = daily maximum temperature, min = daily minimum temperature and T = developmental threshold temperature. Although simple, this method has been used successfully for predicting events relating to decision making for insect control (AliNiazee 1979). Second, the modification proposed by Lindsey and Newman (1956) was tested which more accurately follows daily temperature fluctuations when the threshold is above the daily minimum. When this occurs the above equation is replaced with:

$$\frac{(\text{min} - T)^2}{2 (\text{Max} - \text{min})}$$

The third method sums thermal units in a manner similar to Lindsey and Newman except on a half-day basis. This method was used to improve timing of control of Lygus (Sevachurian et al. 1977).

The accuracy of prediction of egg hatch using the thermal constants obtained from the constant temperature study was compared to the lowest C.V. using the same field development data set.

RESULTS AND DISCUSSION

Oviposition behavior

Oviposition on the upper sides of red raspberry leaves began within 24 hours after placement of virgin females and males inside the

cages. Peak egg laying occurred within two or three days, despite large differences in temperature between the first two and final trials begun on July 14, September 11, and October 10 (Figure 6). This indicates that low temperatures did not lengthen the interval required for pre-oviposition. Some egg masses were laid even when daily low temperatures were at or below freezing and mean temperatures were 7°C (45°F) during the trial begun on October 10. Apparently these low temperatures did have some effect in suppressing the rate of oviposition, however.

Of the total 7,148 eggs oviposited, 50% were deposited by the third and 90% by the ninth day after introduction of the adults into the oviposition cage (Figure 7). The rapid oviposition rate suggests that oviposition behavior is not inhibited by caging or crowding.

Fecundity averaged 296 eggs per female. An average of 383 eggs per female was observed for the replication begun on July 14. An average of only 233 was obtained for the trial begun on October 10. The lower figure could be due to early mortality of some moths caused by lower temperatures or precipitation which occurred during this time (Table 19).

The average number of eggs per egg mass decreased over time in a manner similar to average daily fecundity. The three egg masses oviposited within 24 hours averaged 68.3 eggs per egg mass while only 23.0 were oviposited after nine days (Figure 7).

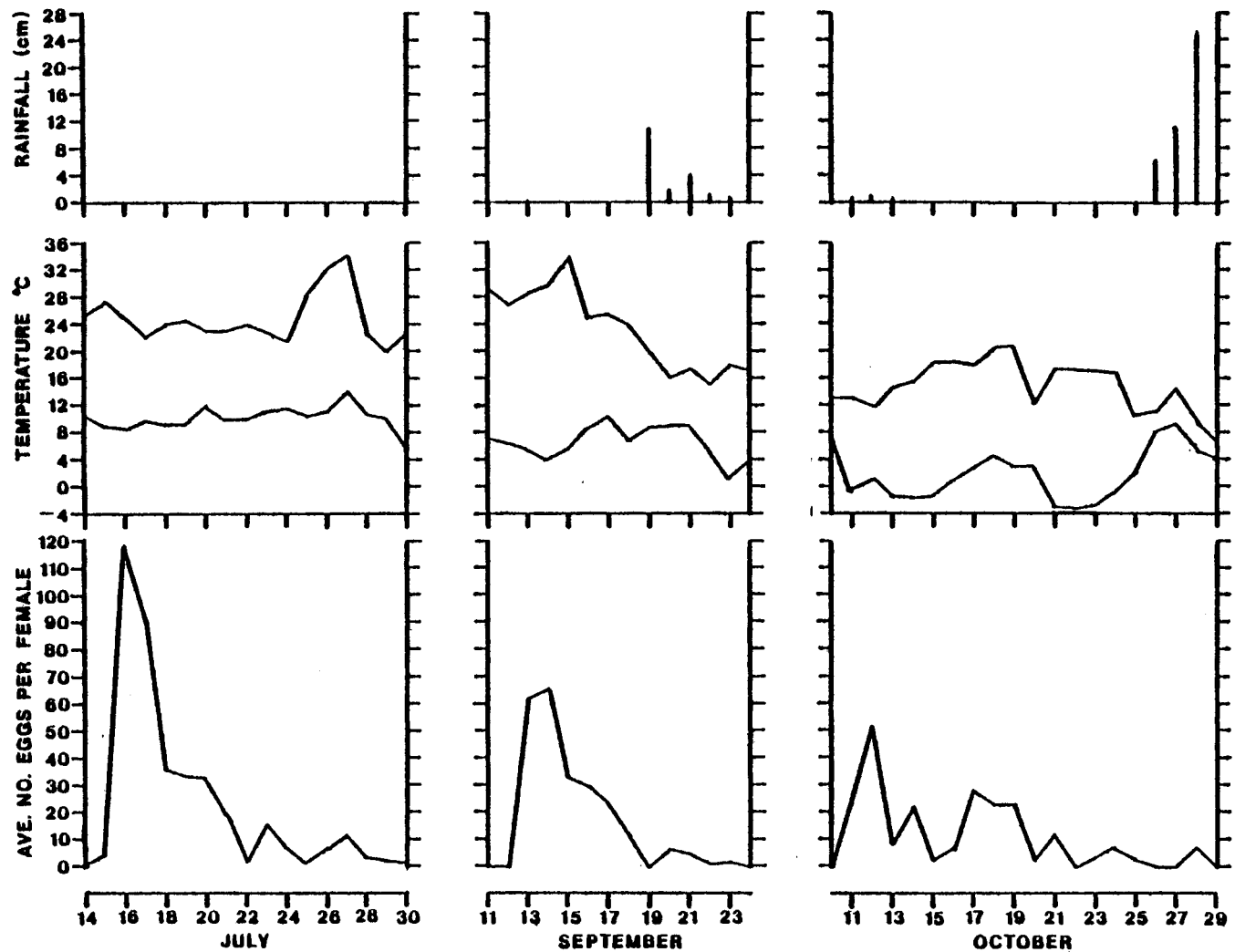


Figure 6. Oviposition record of orange tortrix adults caged in the field at Corvallis, OR on July 14, September 11, and October 10, 1981; with record of daily temperature extremes and precipitation.

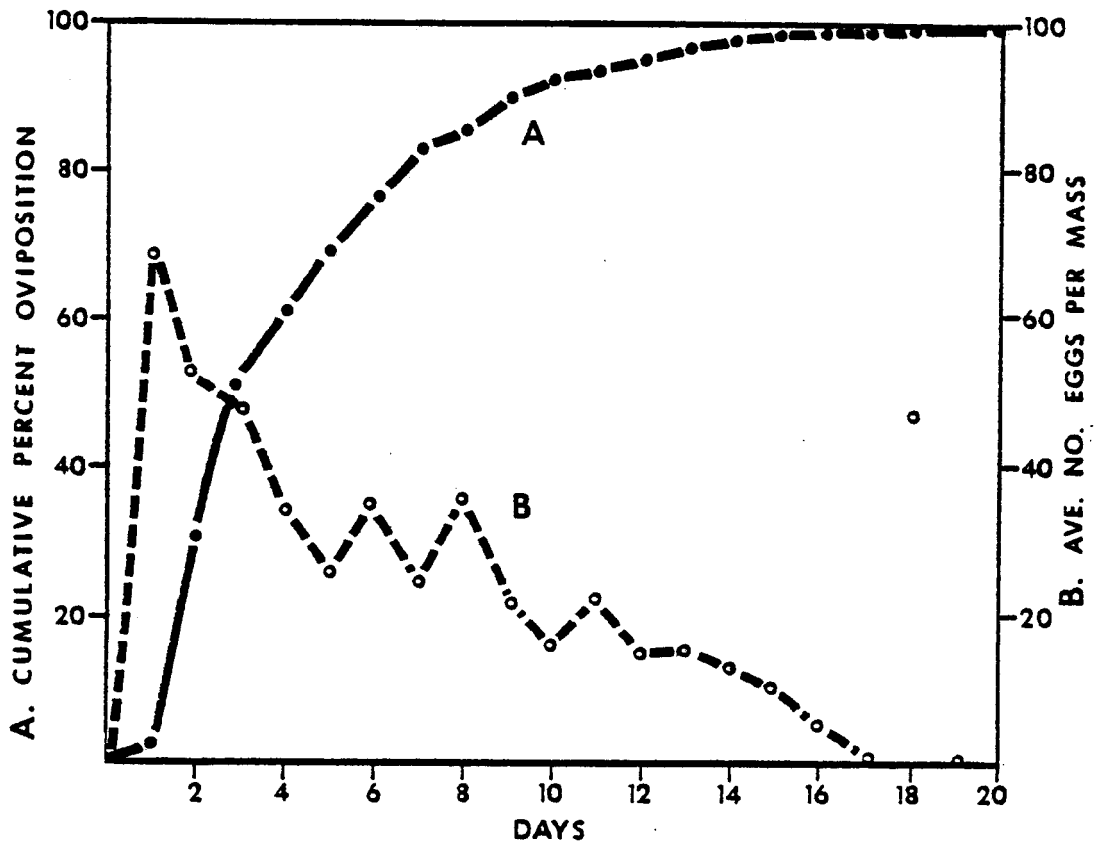


Figure 7. Orange tortrix cumulative percent oviposition (A) and average egg mass size (B), combined for three replicates; July 14, September 11, and October 10, 1981 Corvallis, OR.

Table 19. Orange tortrix field oviposition on caged red raspberries

Date	N ^a	avg. no. per female			environmental conditions during 90% oviposition		
		eggs	egg masses	eggs per egg mass	interval, days	mean temp. °C ^b	precip. cm
7/14	10	383.4	11.9	32.2	9	17.1	0.0
9/11	7	240.4	6.4	37.4	7	17.4	0.0
10/10	7	233.4	6.1	38.0	13	8.5	0.3
total	24	295.9	8.2	36.0	9	-	-

^aNumber males and females caged.

^bAvg. of daily mean temperatures for no. of days indicated.

Egg Development at Constant Temperatures

Successful development occurred for the egg stage of the orange tortrix at all temperatures except 32°C, at which 100% mortality occurred. The average number of days, range and standard deviation for development time are given in Table 20. Developmental rate was greatest at 28°C, with only 7.2 days required for hatch. The lowest temperature used in the study, 12°C, was the only one at which a considerable degree of variation in development time occurred, ranging from 30.0 to 37.5 days. Differences in eclosion time within an egg mass were minimal, with no more than two or three hours difference observed for temperatures greater than 12°C. Survival was good at all temperatures below 32°C, ranging from 97.2% at 20°C to 73.7% at 28°C.

The relationship between temperature and percent development per day, plotted in Figure 8, was nearly linear for the range of temperatures used in this study. Using least-squares linear regression (x-intercept method), the developmental threshold and thermal requirement for egg hatch were estimated to be 7.2°C and 139.4°C-days, respectively. Data from Basinger's (1938) egg development study are also plotted in Figure 8. Basinger found that development occurs at temperatures as extreme as 7.2°C and 29.4°, but with high mortality rates. When regression coefficients derived from the present study and Basinger's were compared by analysis of variance, no significant difference was indicated (Appendix 6).

Table 20. Percent hatch and development period for orange tortrix eggs taken from females held at 20°C and incubated at various temperatures.

Temperature °C	No. egg masses	No. eggs	Percent hatch	Dev. time in days $\bar{X} \pm SD$
12.0	15	793	86.5	33.5 \pm 2.27
16.0	8	432	93.5	15.6 \pm 0.52
20.0	15	1082	97.2	10.6 \pm 0.68
24.0	15	890	89.4	7.5 \pm 0.42
28.0	14	606	73.4	7.2 \pm 0.32
32.0	11	-	0.0	-

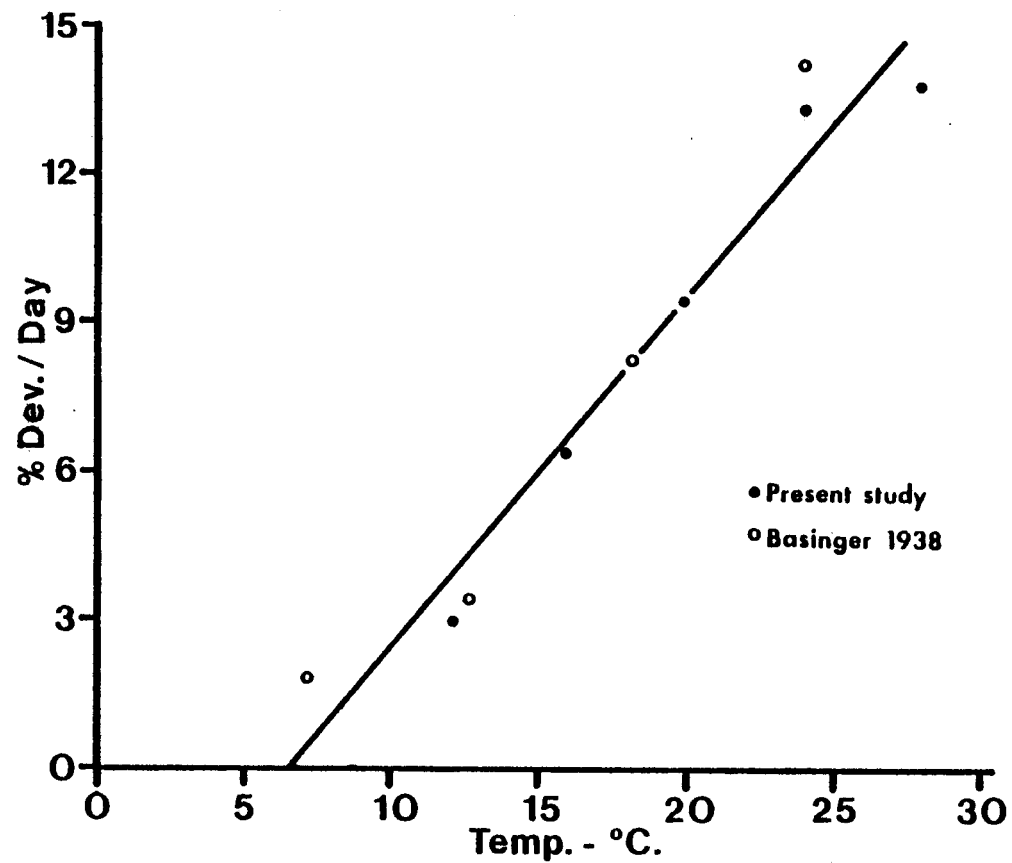


Figure 8. Development rate of orange tortrix eggs in relation to constant temperature.

Egg Development Under Field Conditions

Results of the field studies on orange tortrix egg development are placed in Table 21. The total number of eggs and percent hatch are given as well as the mean and standard deviation of time for development. As evidence that the two slightly different methods used for incubation were essentially the same, results are included from the date July 17, when Stevensen screen incubation was performed in addition to the more natural situation on raspberry leaves. The differences between these two incubation methods were negligible except that development was more variable on the raspberry leaves, which was probably an effect due to greater microclimatic variability. Considering only these four replications, development time ranged from 11.5 days during July to 22 days for eggs oviposited on September 10. Survival was high, ranging from 79.1 to 98.1%.

As in the laboratory egg development studies, development differed primarily in the amount of variation between different egg masses while little variability in eclosion time within egg masses was observed.

An additional replication which began on October 12th was terminated just prior to eclosion by sub-freezing temperatures which occurred during the last week in November. Although embryos within the eggs appeared fully developed at this time and some had already eaten their way out after 41 days, the majority were not able to survive.

Table 21. Percent hatch and developmental period for field incubation of orange tortrix eggs; Corvallis, OR 1981.

oviposition date	location	No. egg masses	no. eggs	percent hatch	dev. time in days $\bar{X} \pm SD$	avg. temp. °C
5/27	plant	5	265	98.1	18.9 \pm 0.55	12.3
6/28	stevenson screen	6	308	79.2	13.2 \pm 0.52	15.8
7/17	plant	8	405	94.8	11.9 \pm 0.44	17.6
7/17	stevenson screen	6	343	93.3	11.5 \pm 0.05	17.6
9/14	plant	8	465	92.8	19.3 \pm 1.07	12.6
10/12	plant	6	-	<5.0	>41	8.3

Estimation of Thermal Constants

Results from the previous study were used to test the developmental threshold and thermal requirement estimates derived from the constant temperature studies as well as to determine which of the most common heat-unit accumulation methods are suitable for predicting egg hatch. Degree-day accumulations for each of the four replications, calculated at five different threshold temperatures are shown in Table 22, along with their means, standard deviations and coefficient of variations. The coefficient of variation (C.V.) was lowest at a 5°C threshold (T) for each of the three methods used to accumulate degree days. Degree-day totals were virtually the same for all three accumulation methods. The least precise method, $(\text{max.} + \text{min.}) / 2 - T$ had the lowest C.V., but overall differences were negligible and it appears from these results that any of the three are suitable for modeling egg development.

Prediction of date of egg hatch based on the linear regression-derived thermal constants, 139°C-days and 7°C, were on the average 4 days late (Table 23). In comparison, prediction of hatch date is only off by an average of 0.5 days by using the thermal constants 146°C-days and 5°C estimated by the lowest C.V. method. This difference serves as an illustration of the necessity for a field validation of thermal constants derived from constant temperature studies. Since the relationship between temperature and developmental rate for insects is essentially sigmoid rather than linear, the selection of which constant temperatures to use can greatly affect the

Table 22. Orange tortrix egg development: Degree day accumulations calculated for five temperature thresholds and three methods of degree day summation; Corvallis, OR.

	threshold temperature ($^{\circ}\text{C}$)				
	3 $^{\circ}$	4 $^{\circ}$	5 $^{\circ}$	6 $^{\circ}$	7 $^{\circ}$
<u>date</u>					
	method 1 ^a				
5/27	178.3	159.3	140.3	121.3	102.3
6/28	168.7	155.7	142.7	129.7	116.7
7/17	177.9	161.4	149.9	138.4	126.9
9/14	189.7	170.2	150.7	131.2	111.7
\bar{X}	178.7	161.7	145.9	130.2	114.4
s	8.60	6.17	5.18	7.02	10.30
C.V.	4.81	3.81	3.55	5.39	8.96
	method 2 ^b				
5/27	178.3	159.5	140.8	122.5	104.5
6/28	168.7	155.7	142.7	129.8	116.9
7/17	172.9	161.4	149.9	138.4	126.9
9/14	189.8	170.6	151.8	133.6	116.2
\bar{X}	177.4	161.8	146.3	131.1	116.1
s	9.14	6.33	5.37	6.71	9.16
C.V.	5.15	3.91	3.67	5.12	7.89
	method 3 ^c				
5/27	177.4	158.6	140.0	121.8	104.0
6/28	168.5	155.5	142.5	129.6	116.9
7/17	173.1	161.6	150.1	138.6	127.1
9/14	189.6	170.5	151.8	133.8	116.6
\bar{X}	177.2	161.6	146.1	131.0	116.2
s	9.06	6.47	5.73	7.12	9.46
C.V.	5.11	4.00	3.93	5.44	8.14

^a $(\text{max} + \text{Min}) \div 2 - T$.

^b (Lindsey and Newman 1956).

^c (Sevacherian et al. 1977).

Table 23. Prediction of orange tortrix egg hatch: thermal constants estimated from linear regression (laboratory data) and by lowest coefficient of variation (field data); Corvallis, OR 1981.

date of oviposition	linear regression method, 7 th threshold					lowest C.V. method, 5 th threshold				
	°C-days		date of hatch		diff., days	°C-days		date of hatch		diff., days
	predicted	actual	predicted	actual		predicted	actual	predicted	actual	
5/27	139	104	6/19	6/14	-5	146	140	6/15	6/14	-1
6/28	139	117	7/13	7/11	-2	146	142	7/11	7/11	0
7/17	139	127	7/29	7/28	-2	146	150	7/28	7/28	0
9/14	139	<u>117</u>	10/11	10/03	<u>-7</u>	146	<u>152</u>	10/02	10/03	<u>+1</u>
ave.		116			-4		146			±0.5

slope when using the linear regression method of thermal constants determination. This is illustrated by the regression estimates calculated from Basinger (1938) data, which closely match the lowest C.V. estimates obtained in the current study (Appendix 1, Table 22). The fitting of an exponential or sigmoid curve to laboratory data has also been used successfully for modeling purposes (Stinner et al. 1974, Reissig 1978), but may involve complex calculations and require temperature data at shorter than daily intervals and thus be less practical. Although an independent data set is needed to more objectively validate the thermal constants derived here, the apparent predictive ability of ± 1 day is probably adequate.

Factors Affecting Prediction of Egg Hatch

The initiation of a degree-day accumulation model for egg development requires that the relationship between pheromone trap catch and oviposition be known. The measurement of this interval was not made directly in this study because of the difficulty in sampling egg masses, so the various factors influencing this interval will be discussed. These factors include; knowledge of emergence pattern differences of the two sexes, the relationship between emergence and trap catch, the interval between emergence and mating and possible associated threshold temperature, and ovipositional behavior.

Emergence Patterns

Although larval development at 21°C requires ca. 3-4 days longer for females, a longer pupal stage for males resulted in the latter's overall developmental rate to be only 1-2 days less at 20°C (Basinger 1938) and 0.7 days less at 24°C (Schwartz and Lyon 1970). Since overwintering generation flight is spread over a period of several months in the field, this difference is probably insignificant. Rearing records for orange tortrix larvae and pupae collected over an extended period during the spring of 1981 can also be examined in regard to this question. If males emerged much earlier than females it would be expected that: 1. Sex ratios of sample populations would shift to higher proportions of females over time, and 2. Males would develop and emerge sooner than females when both are allowed to complete development in the laboratory. Table 24 shows emergence of orange tortrix adults from four larval and pupal samples of the overwintered generation taken at 3 week intervals. Sex ratios did not shift in favor of females over time, and no significant differences in time to emergence between sexes occurred ($P > .05$). The use of emergence traps in the field is recommended to substantiate sexual differences for first emergence, since these samples were not taken early enough to cover this event.

The relationship between emergence and pheromone trap catch should be investigated for the orange tortrix. Although a high correlation between these two events was observed for the codling moth Laspeyresia pomonella (L.) during first flight, factors such as female competition were believed to be responsible for a failure of trap

Table 24. Emergence of overwintering generation orange tortrix collected at Woodland, WA, 1981.

Collection date	Number emerged		Sex ratio ♀:♂	Number of days until emergence ^{a,b} $\bar{X} \pm SE$	
	♀	♂		♀	♂
March 2	36	27	1.3:1.0	21.8±0.79	18.6±1.79
March 23	42	41	1.0:1.0	22.7±1.21	21.8±0.98
April 14	76	63	1.2:1.0	14.8±0.87	13.0±0.66
May 5	44	42	1.1:1.0	9.6±1.18	9.6±0.92

^a Reared at 20±1°C, LD 16:8.

^b Averages within all sample dates are not significantly different at the 0.05 level (t-test).

catch to mimic emergence later in the summer (Riedl et al. 1976). A strong linear correlation throughout spring generation flight was shown for the oriental fruit moth, Grapholitha molesta (Busck), however (Baker et al. 1980).

Interval Between Emergence and Mating; Flight Temperature Threshold

Although the present caging study and Basinger's (1938) findings show the capability of both sexes to mate within 24 hours after emergence, the question of what occurs under completely natural conditions remains to be answered. Probably when economically threatening populations occur, densities will be high and the interval relatively short. Several abiotic factors are known to effect adult flight and mating activity of the codling moth. These include temperature, relative humidity, wind, and precipitation (Shelford 1927, Borden 1931, Pristavco 1969). Of these, temperature has been shown to be one of the more important factors involved (Batiste et al. 1973). Studies on orange tortrix male flight by Riedl and Croft (Unpub.) showed that moths fly at temperatures as low as 10°C. They suggested that A. citrana has a lower temperature threshold and optimum for flight activity than the codling moth, for which 12-13°C was reported (Batiste et al. 1973). The oriental fruit moth has a lower threshold of 15°C for flight as well as female calling (Baker et al. 1980, Baker and Carde 1979). Male orange tortrix moths have been recorded in significant numbers in pheromone traps as early in the spring as March in Oregon, which also indicates that the species is active at relatively low temperatures.

From results of this study on how temperatures influence orange tortrix oviposition, it appears that the ovipositional temperature threshold is also below that observed for the codling moth. During the orange tortrix caging study, eggs were laid at daily mean temperatures as low as 7°C. Oviposition in the laboratory was successful at constant temperatures of 11°C and 9°C. It appears that the orange tortrix is more similar in this regard to Adoxophyes orana (F.v.R.), which has a minimum temperature for oviposition of 11°C (Minks and de Jong 1975). In contrast, a threshold of 18.3°C has been observed for oviposition activity by the codling moth (Parker 1959). In the orange tortrix caging study, no preovipositional period was required even for a mean temperature of 8°C, and oviposition peaked within two to three days following emergence.

Although egg masses could not be sampled for verification, the preceding evidence suggests that oviposition activity begins with little delay following continuous pheromone trap catches. Such a pattern was seen for the summer fruit tortrix, Adoxophyes orana (F.v.R.), for which temperature recordings were begun 2 or 3 days after the regular appearance of moths in pheromone traps for a physiological time model predicting egg hatch (Minks and de Jong 1975). It is recommended that first hatch of the orange tortrix be predicted by initiating heat unit accumulations after a similar interval of only a few days. However, the optimal time for control is probably not the event of first hatch for the orange tortrix. Knowledge of this event merely provides additional information for

making proper control decisions. For example, first egg hatch was not predicted until May 25 in Corvallis, OR in 1980, which occurred after initial red raspberry bloom. Thus a recommended pre-bloom cover spray would not have been properly timed for newly-hatched larvae.

Validation of a model predicting events such as 50% egg hatch may be deterred by problems associated with interpretation of pheromone traps and sampling eggs and young larvae. A phenology model of the complete life cycle, such as is now being developed through the PETE system (Welch et al. 1978) can alleviate this problem however. It can also serve field consultants and growers in understanding the biology of the orange tortrix.

When it becomes more fully defined how the population is distributed in the various life stages over time, control efforts will become more successful since timing will be adjusted to when a greater portion of the population is susceptible.

SUMMARY

Oviposition activity of field caged females began within 24 hours and peaked within 3 days after emergence. Of total eggs produced, 90% were oviposited within 9 days, although activity was suppressed somewhat when daily mean temperatures were less than 7°C. Average size as well as no. of egg masses per day decreased over time.

Egg development at constant temperatures closely matched results obtained by Basinger (1938). Incubation required from 33.5 days at 12°C to 7.2 days at 28°C; none survived at 32°C. Development time in

the field took from 11.5 to greater than 41 days for eggs deposited July 17 and October 12. By the method of lowest coefficient of variation, thermal constants were determined to be 5°C and 146 degree-days. The simplest method of degree-day accumulation, $(\text{max} + \text{min. daily temp.}) / 2 - 5^{\circ}\text{C}$ was suitable.

These results and additional field data were discussed in regard to the potential for predicting egg hatch based upon pheromone trap catch. It was concluded that first hatch could be reasonably predicted using information presently known.

BIBLIOGRAPHY

- AliNiazee, M.T. 1979. Bionomics and life history of a filbert leafroller, Archips rosanus (Lepidoptera:Tortricidae). Ann. Entomol. Soc. Am. 70(3):391-401.
- AliNiazee, M.T. 1979. A computerized model for predicting biological events of Rhagoletis indifferens (Diptera: Tephritidae) Can. Entomol. 11:1101-1109.
- Anonymous. 1926. Entomological work of the year. Rep. Calif. Agri. Expt. Sta. 1924-5. Berkeley Calif. pp. 43-46 and 51-53.
- Anonymous. 1930. First record of Argyrotaenia citrana (Fern.) in Washington. Insect Pest Survey Bull., 9(6):246.
- Anonymous. 1980, 1981. Climatological data, Washington and Oregon, U.S. Dept. of Commerce, Weather Bureau.
- Arnaud, P.H. 1978. A host-parasite catalog of North American Tachinidae (Diptera). U.S.D.A. Misc. Pub. No. 1319.
- Arnold, C.Y. 1959. The determination and significance of the base temperature in a linear heat unit system. Proc. Am. Soc. Hortic. Sci. 74:430-445.
- Baker, T.C. and R.T. Carde. 1979. Endogenous and exogenous factors affecting periodicities of female calling and male sex pheromone response in Grapholitha molesta (Busck). J. Insect Physiol. 25:943-950.
- Baker, T.C., R.T. Carde and B.A. Croft. 1980. Relationships between pheromone trap capture and emergence of adult oriental fruit moths, Grapholitha molesta (Lepidoptera: Tortricidae). Can. Entomol. 112:11-15.
- Bartges, R.J. 1951. Studies concerning the synonymy of two tortricid moths, Argyrotaenia citrana (Fernald) and Argyrotaenia franciscana (Walsingham). Ph.D. thesis, Univ. Calif. (unpublished). 76 pp.
- Basinger, A.J. 1935. Parasites reared from Argyrotaenia citrana. Calif. agri. Mo. Bull. XXIV:233-234.
- Basinger, A.J. 1938. The orange tortrix Argyrotaenia citrana. Hilgardia 11 (11):635-669.

- Bastiste, W.C., W.H. Olson and A. Berlowitz. 1973. Codling moth: Influence of temperature and daylight intensity on the periodicity of daily flight in the field. *J. Econ. Entomol.* 66:883-892.
- Borden, A.D. 1931. Some field observations on codling moth behavior. *J. Econ. Entomol.* 24:1137-45.
- Boyce, A.M. and J.C. Ortega. 1947. Control of orange worms. *Calif. Citrograph* 32 (7):318-319.
- Breakey, E.P. and G.S. Batchelor. 1948. The orange tortrix, a pest of raspberries in western Washington. *J. Econ. Entomol.* 41(6): 805-806.
- Breakey, E.P. 1951. Natural control of the orange tortrix in western Washington. *J. Econ. Entomol.* 44(3):424.
- Campbell, A., B.D. Frazer, N. Gilbert, A.P. Gutierrez and M. Mackauer. 1974. Temperature requirements of some aphids and their parasites. *J. Appl. Ecol.* 11:431-438.
- Cantwell, G.E. and B.A. Franklin. 1966. Inactivation by irradiation of spores of Bacillus thuringiensis var. thuringiensis. *J. Invert. Pathol.* 8:256-258.
- Carlson, R.W. 1979. Ichneumonoidea. In Krombein et al. Catalog of Hymenoptera in America north of Mexico. Smithsonian Inst. Press, Wash. D.C. 1:315-741.
- Chmiel, S.M. and M.C. Wilson. 1979. Estimation of the lower and upper developmental threshold temperatures and duration of the nymphal stages of the meadow spittlebug, Philaenus spumarius. *Environ. Entomol.* 8(4):682-685.
- Claret, J. 1973. La diapause facultative de Pimpla instigator (Hymenoptera, Ichneumonidae) I. Role de la photoperiode. *Entomophaga* 18(4):409-418.
- Clausen, C.P. 1940. Entomophagous Insects. Hafner Pub. Co. N.Y. 688 pp.
- Coquillett, D.W. 1894. Report on some of the injurious insects of California. The orange leafroller (Tortrix citrana, Fernald) p. 24 In: Riley, C.V. Reports of observations and experiments in the practical work of the division. U.S. Dept. Agri. Div. *Entomol. Bull.* 32 (o.s.):1-59.

- Coudriet, D.L. 1970. Rearing the orange tortrix on a synthetic diet. J. Econ. Entomol. 63 (3):1004-1005.
- Ebeling, W. and R.J. Pence. 1957. Orange tortrix on avocados. Calif. Agri. 11(8):13-14.
- Essig, E.O. 1926. Insects of Western North America. The Macmillan Co. New York. 1035 pp.
- Fernald, C.H. 1889. North America microlepidoptera, Tortrix citrana, New Sp. Entomol. American. 5(1):18.
- Flanders, S.E. 1930. Notes on Trichogramma minutum Pan-Pac. Entomol. 6(4):180-181.
- Frick, K.E. and R.F. Wilson. 1981. Head capsule measurements of Bactra verutana larvae reared on an artificial diet. Environ. Entomol. 10:237-239.
- Griego, V.M. and K.D. Spence. 1978. Inactivation of Bacillus thuringiensis spores by ultraviolet and visible light. Appl. Environ. Microbiol. 35(5):906-910.
- Hill, A.S., R.T. Carde, H. Kido and W.L. Roelofs. 1975. Sex pheromone of the orange tortrix moth, Argyrotaenia citrana (Lepidoptera: Tortricidae). J. Chem. Ecol. 1(2):215-224.
- Johansen, C. and E.P. Breakey. 1949. Accumulated residues of insecticides tested to control the orange tortrix on red raspberries. J. Econ. Entomol. 42(3):543.
- Johansen, C. 1978. Insect pests of small fruit. in: Fundamentals of Applied Entomology. 3rd edition. Macmillan Pub. Co. N.Y. 798 pp.
- Kieffer, J.N. 1979. Insect and spider population on red raspberries, Rubus idaeus (Linnaeus), and factors influencing their level as contaminants in mechanically harvested berries. M.S. Thesis (unpublished) Wash. St. Univ. 70 pp.
- Kido, H., D.L. Flaherty, C.E. Kennett, N.F. McCalley and D.F. Bosch. 1981. Seeking the reasons for differences in orange tortrix infestations. Calif. Agri. 34(4):27-29.
- Kido, H., E.M. Stafford and N.F. McCalley. 1971. Orange tortrix on grapes in Salinas Valley. Calif. Agri. 25(7):10-11.

- Krombein, K.V., P.D. Hurd, Jr., D.R. Smith and B.D. Burks. 1979. Catalog of Hymenoptera in America North of Mexico. Vols., 1,3. Smithsonian Inst. Press, Wash. D.C.
- Lange, W.H. 1936. The biology of the orange tortrix Eulia (Argyrotaenia) citrana Fernald Cal. St. Dept. Agri. Mo. Bull. 25(2):283-285.
- Lindsey, A.A. and J.E. Newman. 1956. Use of official weather data in spring-time temperature analysis of an Indiana phenological record. Ecology. 37(4):812-823.
- Lyon, R.L., C.E. Richmond, J.L. Robertson and B.A. Lucas. 1972. Rearing diapause and diapause-free western spruce budworm (Choristoneura occidentalis) (Lepidoptera: Tortricidae) on an artificial diet. Can. Entomol. 104:417-26.
- McGugan, B.M. 1955. Certain host-parasite relationships involving the spruce budworm. Can. Entomol. 87:178-187.
- McLeod, D.G.R. and S.D. Beck. 1963. Photoperiodic termination of diapause in an insect. Biol. Bull. 124:84-96.
- Madsen, H.F., A.D. Borden and R.E. Clark. 1953. Orange tortrix on apricots. Calif. Agri. 7(12):7-8.
- Madsen, H.F. and L.B. McNelly. 1961. Important pests of apricots. Calif. Agri. Exp. Sta. Bull. 783. 40 pp.
- Miller, C.A. 1966. The black-headed budworm in Eastern Canada. Can. Entomol. 98:592-613.
- Minks, A.K., D.J. deJong. 1975. Determination of spraying dates for Adoxophyes orana by sex pheromone traps and temperature recordings. J. Econ. Entomol. 68(5):729-732.
- Morris, K.R.S. 1937. The prepupal stage in Ichneumonidae. Bull. Entomol. Res. 28:525-534.
- Neter, J. and W. Wasserman. 1974. Applied linear statistical models. Irwin Inc. Homewood, Ill. 842 pp.
- Parker, R.L. 1959. Notes on oviposition behavior responses of the codling moth, Carpocapse pomonella L., to air movement, temperature, and light. J. Kansas Entomol. Soc. 32:152-154.
- Penny, D.D. 1921. A skin feeding tortricid, Cacoecia franciscana (Wlsh.) injurious to apples in the Pajaro Valley. Calif. Dept. Agri. Mo. Bull. 10(4):146-150.

- Poonyathawoni, P. 1968. Insect parasites of the omnivorous leaf-tier, Cnephasia longana (Haworth) in Oregon. M.S. Thesis (Unpub). Oreg. State Univ. 56 pp.
- Powell, J.A. 1964. Biological and taxonomic studies on tortricine moths, with reference to the species in California. Univ. of Calif. Pubs. in Entom. Vol 32. Univ. Calif. Press Berkeley. 317 pp.
- Pristavco, U.P. 1969. Evaluation of some abiotic factors influencing captures of codling moths by black-light traps. J. Zool. 48: 1177-1184.
- Quayle, H.J. 1910. The orange tortrix, Tortrix citrana Fernald. J. Econ. Entomol. 3(5):401-403
- Quayle, H.J. 1938. Insects of citrus and other subtropical fruits. Comstock Publishing Co. pp. 206-211.
- Reissig, W.H. 1978. Biology and control of the obliquebanded leafroller on apples. J. Econ. Entomol. 71:804-809.
- Riedl, H., B.A. Croft and A. J. Howitt. 1976. Forecasting codling moth phenology based on pheromone trap catches and physiological-time models. Can. Entomol. 108:449-460
- Rosenstiel, R.G. 1949. Life history and control of the orange tortrix in Oregon. J. Econ. Entomol. 42(1):37-40.
- Saunders, D.S. 1976. Insect clocks. Pergamon Press. N.Y. 279 pp.
- Schuh, J. and D.C. Mote. 1948. The obliquebanded leafroller on red raspberries. Oreg. Agri. Exp. Sta. Tech. Bull. 13:1-43.
- Schwartz, J.L. and R.L. Lyon. 1970. Laboratory culture of orange tortrix, and its susceptibility to four insecticides. J. Econ. Entomol. 63(6):1788-1790.
- Schwenke, W. 1956. Local dependence of parasitic insects and its importance for biological control. Proc. 10th Int. Cong. Entomol. 4:851-854.
- Sevacherian, V., V.M. Stern and A.J. Mueller. 1977. Heat accumulation for timing lygus control measures in a safflower-cotton complex. J. Econ. Entomol. 70:399-402.
- Shelford, V.E. 1927. An experimental investigation of the relations of the codling moth to weather and climate. Ill. Nat. Hist. Serv., Vol. XVI, Art. V.

- Smilowitz, Z. and G.F. Iwantsch. 1973. Relationships between the parasitoid Hyposoter exiguae and the cabbage looper Trichoplusia ni: Effects of host age on developmental rate of the parasitoid. Environ. Entomol. 2:759-763.
- Smith, S.M. and R.A. Brust. 1971. Photoperiodic control of the maintenance and termination of larval diapause in Wyeomyia smithii (Coq.) (Diptera: Culicidae) with notes on oogenesis in the adult female. Can. J. Zool. 49:1065-1073.
- Solomon, M.E. 1951. Control of humidity with potassium hydroxide, sulphuric acid, or other solutions. Bull. Entomol. Res. 42:543-554.
- Stinner, R.E., A.B. Gutierrez and G.D. Butler, Jr. 1974. An algorithm for temperature-dependent growth rate simulation. Can. Entomol. 106:519-524.
- Tauber, M.J. and C.A. Tauber. 1973. Quantitative response to day-length during diapause in insects. Nature. 244(3):296-297.
- Tauber, M.J. and C.A. Tauber. 1976. Insect seasonality: diapause maintenance, termination, and postdiapause development. Ann. Rev. Entomol. 21:81-107.
- Townes, H. and M. Townes. 1959. Ichneumon-flies of America. 1. Metopiinae. U.S. Natl. Mus. Bull. 216 [pt. 1]:170-221.
- Townes, H. 1969. Ichneumonidae as biological control agents. Proc. Tall Timbers Conf. on Ecol. Anim. Cont. 1:235-248.
- Vinson, S.B. 1976. Host selection by insect parasitoids. Ann. Rev. Entomol. 21:109-132.
- Vinson, S.B. and G.F. Iwantsch. 1980. Host regulation by insect parasitoids. Quart. Rev. Biol. 55(2):143-65.
- Welch, S.M., B.A. Croft, J.F. Brunner and M.F. Michels. 1978. PETE: an extension phenology modeling system for management of multi-species pest complex. Environ. Entomol. 7(4):487-494.
- Zeller, S.M. and J. Schuh. 1944. Diseases and insect pests of cane fruits. Fruits in Oregon. Oreg. Exp. Sta. Bull. 478.

APPENDICES

Appendix 1. Regression equations and thermal constant estimates for orange tortrix development based on Basinger (1938) constant temperature studies, range 7.2-23.9°C.

Stage	Regression equation ^a	Temperature threshold °C ^b	°C-days ^c	R ²	°C-days @ T _d = 5°C
Egg	Y = .007629x - .04903	6.4	131.1	.95	144.9
Larva	Y = .002325x - .00975	4.2	430.2	.99	408.2
Pupa	Y = .005699x - .02718	4.8	175.5	.99	172.8
Total	Y = .001368x - .00677	5.0	731.0	.98	728.7

^aRegression equation is $Y = mx + b$ where Y is proportion of development per day and x is temp. in °C.

^bDevelopmental threshold temp. is x-intercept of regression equation ($= -b/m$).

^cThermal requirement is reciprocal of slope of regression equation ($= 1/m$).

Appendix 2. Summary of orange tortrix larval parasitism between May 26 and Oct. 22, 1980-1981 for samples where at least ten larvae were reared.

		Numbers reared ¹														
Location	Date	No. larvae coll.	No. per hour	No. reared	Total parasitized		A.a.	M.a.	P.v.	E.e.	D. spp.	O.a.	P.g.	M.d.	Others	
<u>1980</u>																
Woodland	July 7	24	36.0	23	1	4.3				1						
	14	73	110.0	68	12	17.6	1	9		1			1			
	21	69	30.7	67	18	26.9	2	10		1			3	2		
	28	66	26.4	66	21	31.8	7	7		2			5			
	Sept. 29	64	21.3	58	18	31.0	7		10		1					
	Oct. 11	105	30.0	100	35	35.0	9	2	19	1	3				1	
<u>1981</u>																
	May 26	21	13.3	21	6	28.6	3			3						
	June 26	124	93.0	124	36	29.0	17	15		1				2	1	
	Sept. 15	40	53.3	39	3	7.7	2		1							
	Oct. 22	20	10.0	20	3	15.0			1						2	
St. Paul	June 12	25	16.7	23	4	17.4		1				3				
	July 22	89	89.0	86	27	31.4	16	6	1	4						
	Sept. 21	40	34.3	39	3	7.7	1		1						1	
	Oct. 22	20	10.0	20	3	15.0			1						2	
Scholls	June 12	15	11.3	13	3	23.1	1	1		1						
	July 22	16	16.0	14	14	100.0	1	10		1		2				
Corvallis Twedts	June 23	19	19.0	18	5	27.8	3			2						
	July 9	37	8.2	34	22	64.7		17	2			3		1		
	Sept. 25	13	5.6	13	3	23.1						3				
	Oct. 10	31	25.0	28	27	96.4		16			11					
Corvallis Ent. farm	July 10	31	25.0	28	27	96.4		16			11					
	Aug. 20	19	19.0	16	9	56.3	4					4			1	
Salem	July 22	15	22.5	11	9	81.8	5			2	1	1				
Junction City	Sept. 18	39	14.5	37	33	89.2	24		1		6				2	
Totals				918	312	34.0	103	94	36	20	22	15	9	5	8	

¹Abbreviations: A.a., Apanteles aristoteliae; M.a., Meteorus argyrotaeniae; P.v., Phytodietus vulgaris; E.e., Enyus eureka; D. spp., Diadegma spp.; O.a., Oncophanes americanus; P.g., Parania geniculata; M.d., Meteorus dimidiatus.

Appendix 3a. Fall rearing records used to evaluate overwintering stages of Apanteles aristoteliae.

Species	Coll loc.	Coll. date	No. orange tortrix larvae coll. and reared	No. reared	Days to cocoon formation ^a $\bar{X} \pm SD$	% of Avg. egg plus larval dev.
<u>Apanteles aristoteliae</u>	Woodland WA	Sept. 29 1980	58	7	13.0 \pm 1.5	63.6%
	Woodland WA	Oct. 11 1980	100	1	1	4.9%
				9	46.3 \pm 9.2	226.4%
	Woodland WA	Nov. 8 1980	64	2	20.0 \pm 4.2	97.8%
	Woodland	Sept. 15	39	2	7.0 \pm 0.0	34.2%
	St. Paul OR	Sept. 21 1981	39	1	9	44.0%
	St. Paul OR	Oct. 22 1981	20	0	-	-

^a Reared at 20 \pm 1°C and LD 16:8 except when collected on Oct. 11, 1980 when 20.0 \pm 2°C and natural photoperiods were used.

Appendix 3b. Spring rearing records used to evaluate overwintering stages of Apanteles aristoteliae.

Species	Coll. loc.	Coll. date	No. orange tortrix larvae coll. and reared	No. reared	Days to cocoon formation ^a $\bar{x} \pm SD$	% of avg. egg plus larval dev.	# days coll. to emergence $\bar{x} \pm SD$
<u>Apanteles aristoteliae</u>	Woodland WA	March 2 1981	56	1	16	78.2%	-
			reared from leaf litter	1	-	-	11
	Woodland WA	March 23 1981	89	3	16.0 \pm 6.6	78.2%	-
	Woodland WA	April 14 1981	63	0	-	-	-
			reared from leaf litter	4	-	-	10.5 \pm 2.6
	Woodland WA	May 05 1981	27	1	9	44.0%	-
			reared from leaf litter	6	-	-	9.8 \pm 5.3
	Woodland WA	May 26 1981	21	4	17.8 \pm 1.5	87.0%	-
	Woodland WA	June 26 1981	124	17	9.3 \pm 2.8	45.5%	-

^aReared at 20 \pm 1°C and LD 16:8.

Appendix 4a. Fall rearing records used to evaluate overwintering stages of Meteorus argyrotaeniae.

Species	Coll. loc.	Coll. date	No. orange tortrix larvae coll. and reared	No. reared	Days to cocoon formation ^a $\bar{X} \pm SD$	% of Avg. egg plus larval dev.
<u>Meteorus</u> <u>argyrotaenia</u>	Woodland WA	Sept. 29 1980	58	0	-	-
	Woodland WA	Oct. 11 1980	100	2	34.5 \pm 23.3	284.0%
	Woodland WA	Nov. 08 1980	64	2	18.0 \pm 7.1	148.0%
	Woodland WA	Sept. 15 1981	39	0	-	-
	St. Paul OR	Sept. 21 1981	39	0	-	-
	St. Paul OR	Oct. 22 1981	20	0	-	-

^a Reared at $20 \pm 1^{\circ}\text{C}$ and LD 16:8 except when collected on Oct. 11, 1980 when $20.0 \pm 2^{\circ}\text{C}$ and natural photoperiods were used.

Appendix 4b. Spring rearing records used to evaluate over-wintering stages of Meteorus argyrotaeniae.

Species	Coll. loc.	Coll. date	No. orange tortrix larvae coll. and reared	No. reared	Days to cocoon formation ^a $\bar{x} \pm SD$	% of avg. egg plus larval dev.	# days coll. to emergence $\bar{x} \pm SD$
<u>Meteorus argyrotaenia</u>	Woodland WA	March 1980	2 56	0	-	-	-
	Woodland WA	March 1980	23 89	2	5.0 \pm 1.4	41.2%	-
			collected cocoon	1	-	-	9
	Woodland WA	April 1981	14 63	1	2	16.5%	-
			reared from leaf litter	1	-	-	9
	Woodland WA	May 1981	5 27	7	12.6 \pm 2.0	103.0%	-
	Woodland WA	May 1981	26 21	0	-	-	-
	Woodland WA	June 1981	26 124	15	11.3 \pm 2.5	93.0%	-

^a Reared at 20 \pm 1°C and LD 16:8.

Appendix 5a. Fall rearing records used to evaluate overwintering stages of Enytus eureka and Diadegma spp.

Species	Coll. loc.	Coll. date	No. orange tortrix larvae coll. and reared	No. reared	Days to cocoon formation ^a $\bar{X} \pm SD$
<u>Enytus eureka</u>	Woodland WA	Oct. 11 1980	100	1	32
	Woodland WA	Nov. 8 1980	64	4	14.0 \pm 2.4
	Corvallis, OR Ent. farm	Nov. 26 1981	7	4	28.3 \pm 14.6
<u>Diadegma</u> spp.	Woodland WA	Sept. 29 1980	58	1	14
	Woodland WA	Oct. 11 1981	100	3	18.3 \pm 4.0
	Junction City, OR	Sept. 18 1981	37	5	9.6 \pm 2.3
	St. Paul OR	Sept. 21 1981	-	1 ^b	30
	St. Paul OR	Oct. 22 1981	-	1 ^b	30

^a Reared at 20 \pm 1°C and LD 16:8 except when collected on Oct. 11, 1980 when 20.0 \pm 2°C and natural photoperiods were used.

^b Host: C. rosaceana.

Appendix 5b. Spring rearing records used to evaluate overwintering stages of Enytus eureka and Diadegma sp.

Species	Coll. loc.	Coll. date	No. orange tortrix larvae coll. and reared	No. reared	Days to cocoon formation ^a $\bar{X} \pm SD$	% of avg. egg plus larval dev.	# days coll. to emergence $\bar{X} \pm SD$
<u>Enytus eureka</u>	Woodland WA	March 23 1981	89	0	-	-	-
			Collected cocoon	1	-	-	9
	Corvallis, OR Hort. Farm	April 3 1981	-	1 ^b	13	-	-
	Filedale WA	May 5 1981	-	1 ^b	10	-	-
<u>Diadegma</u> spp.	Corvallis, OR Hort. Farm	April 3 1981	-	4 ^b	12.3 \pm 2.6	-	-
	Corvallis OR Hort. Farm	April 12 1981	-	4 ^b	16.3 \pm 1.0	-	-
	Woodland WA	April 14 1981	63	2	12.0 \pm 1.4	-	-

^a Reared at 20 \pm 1°C and LD 16:8.

^b Host: C. rosaceana.

Appendix 6. Parameters used to simulate Apanteles aristoteliae phenology by the PETE model.

	Degree-days for dev.	Overwintering stages												
Stage		1	2	3	4	5	6	7	8	9	10	11	12	
Egg	60	0	0	0	0	0	0	0	0	0	0	0	0	
Larva	334	5	5	5	5	6	6	6	6	6	6	6	6	
Pupa	206	0	0	0	0	0	0	0	0	0	0	0	0	
Pre-ov	15	0	0	0	0	0	0	0	0	0	0	0	0	
Adult	200	0	0	0	0	0	0	0	0	0	0	0	0	
		13	14	15	16	17	18	19	20	21	22	23	24	25
Egg		0	0	0	0	0	0	0	0	0	0	0	0	0
Larva		6	6	5	5	5	5	0	0	0	0	0	0	0
Pupa		0	0	0	0	0	0	0	0	0	0	0	0	0
Pre-ov		0	0	0	0	0	0	0	0	0	0	0	0	0
Adult		0	0	0	0	0	0	0	0	0	0	0	0	0

Temperature Thresholds: Flytemp = 60°F
 K1 = 49°F.
 K2 = 86°F.
 K3 = 0°F.

Delta Degree Days = 2.50

BIOFIX: Date = 1/1 BFXDD = 1.00

Appendix 7. Comparison of regression coefficients by analysis of variance for present and Basinger's (1938) studies on orange tortrix egg development. Method of Neter and Wasserman (1974), pp. 160-165.

I. Full Model

i. Basinger 1938. Temperature range 7.22 - 23.89°C.

Source	SS	df	MS	F	Regression coefficients:
Regression	.008983	1	.008983	37.04*	bo1 = -0.049029
Error	.0004850	2	.0002425		bo2 = 0.007629
Total	.009468	3			r ² = 0.95

ii. Present study. Temperature range 12.0 - 28.0°C.

Source	SS	df	MS	F	Regression coefficients:
Regression	.008231	1	.008231	83.20***	bo1 = -0.051350
Error	.0002968	3	.00009893		bo2 = 0.007173
Total	.008528	4			r ² = 0.96

$$SSE(F) = SSE_1 + SSE_2 = .0007818$$

II. Reduced Model

Source	SS	df	MS	F	Regression coefficients:
Regression	.08112	1	.08112	557.91***	bo1 = -0.04604
Error	.001018	7	.0001454		bo2 = 0.007110
Total	.01913	8			r ² = 0.95

$$\text{Test statistic } F = \frac{SSE(R) - SSE(F)}{2} \div \frac{SSE(F)}{n_1 + n_2 - 4}$$

$$F = 0.76 \text{ N.S.}$$

* Significant at .05.

*** Significant at .005.