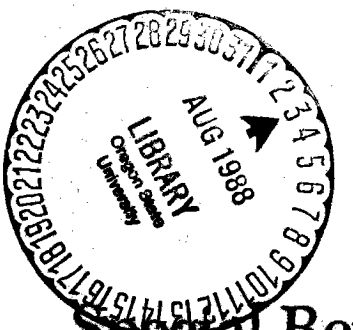
Ecology and Management of Economically Important Fruit Flies



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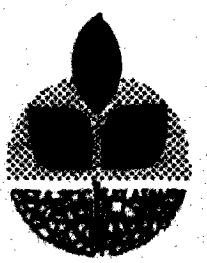

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ECOLOGY AND MANAGEMENT

OF

ECONOMICALLY IMPORTANT FRUIT FLIES

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PREFACE

This volume is a proceeding of the papers presented in an "Informal Conference" during the Annual Meetings of the Entomological Society of America held on December 8, 1985, in Hollywood, Florida. Although most of the papers presented during the conference are included in this publication, there were three additional papers which are not presented here since they have been published elsewhere.

Our goal was to bring together leading scientists from North America working on Tephritid fruit flies to present a progress report on their respective research and provide a general overview of the subject. We were fortunate that most of the leading laboratories were able to present their recent findings during the "Conference." In addition, some very interesting talks were presented on detection, eradication, and quarantine of the fruit flies. By no means is it a comprehensive book on current research on Tephritid flies, but it does provide an excellent overview of ecology, quarantine, and integrated management of some important Tephritid flies of North America. Of special interest are chapters on quarantine and eradication of fruit flies from the high-hazard areas of California and Florida.

This informal conference was made successful by enthusiastic participation of different scientists from across North America. Sincere appreciation is extended to all those who participated in the conference, formally and informally.

January 1987

M. T. AliNiazee
Corvallis, Oregon

CONTENTS

CHAPTER 1

Introduction

M. T. AliNiazee

The fruit flies of the family Tephritidae are among the most serious pests of agricultural crops throughout the world. From a small mango grove in tropical Asia to the large commercial apple farmers of north America, the problem is the same. Small picturous flies, depositing eggs inside the fruit, hatched larvae feeding on fruit flesh rendering it unsuitable for consumption. Although accurate estimates of damage are difficult to come by, economists at the California Department of Food and Agriculture were estimating a potential loss of nearly $15 billion if the Mediterranean fruit fly, *Ceratitis capitata* (Wied.), had gotten established in that State permanently (Hagen et al. 1981). Similarly, it is estimated that the recent establishment of the apple maggot, *Rhagoletis pomonella* (Walsh), in the Pacific Northwest could cause as much as $30-40 million economic loss per year (AliNiazee and Penrose 1981).

Among the reasons that make the fruit flies such serious pests include their direct larval feeding on the host fruit (vs. foliar feeding); their long list of host plants (particularly true with tropical fruit flies); their flexibility in developing different life history strategies, including rapid adaptation to new habitats; efficient habitat utilization; an ability to rapidly develop host and geographic races (particularly true with the *Rhagoletis* species); and their short generation time (especially true with tropical fruit flies).

In spite of these serious problems, the control measures remained practically unchanged for almost 30 years. These include; a) sprays of persistent pesticides, ground and ultra low volume (ULV); b) bait sprays using protein hydrolysates or other types of attractants mixed with an insecticide; c) quarantine; and d) eradication. Better utilization of traps and phenology models has undoubtedly helped in more precise timing of the use of pesticides; however, very few alternative methods have yet been developed. In spite of some interesting results with oviposition deterring pheromones (ODP), no commercial utilization of this technique seems yet possible.

The success of SIT in controlling certain tropical fruit flies has been excellent, if not spectacular (La Chance et al. 1967). The use of SIT along with aerial application of short-lived organophosphate (OP) compounds now form the basis of every fruit fly eradication program, including those pursued in such

high-hazard states as California and Florida. Success of SIT as an IPM tactic solely or in combination with other methods has been mixed. Relatively better results were obtained with the tropical fruit flies than with the temperate flies (Cavalloro, 1983). Logistical problems such as adequacy of mass rearing, sterilization and distribution methods, biological problems such as quality control, inadequate ecological understanding, crop production methodology, and lack of financial support may be the most important hindrance in this regard.

The success of biological control measures against Tephritid flies has been limited in spite of early optimism echoed by Clausen (Clausen 1958). In part, because of an extremely low economic tolerance level, the biological control does not seem to provide an adequate alternative as a sole control. However, it can provide effective suppression of population under natural conditions, thus reducing the available reservoir. Working with *R. indifferens*, Dr. Hagen and I have shown that as much as 70-80 percent parasitization of this insect could occur under field conditions repeatedly. However, the remaining 20-30 percent of the population was sufficient to cause economic loss in most orchards. Similarly, a large number of apple maggot adults were parasitized by two opiine parasitoids in Oregon (AliNiazee 1985), but not enough to provide commercial control.

The new research dealing with the attractants and volatiles and their utilization in trapping and control programs is one of the bright areas of the fruit fly research. Also, the behavior and host selection work being conducted by Dr. Prokopy's laboratory may help in developing alternative methods for controlling these flies. Some very interesting work dealing with bacterial symbionts is coming out of Australia (Drew et al. 1984). Hopefully, within the next 5-10 years, we will have a much better understanding of these pestiferous flies and would be able to manage them better than what we do now.

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CHAPTER 2

The Fruit Fly Problem in Hawaii

Wallace C. Mitchell

On the average, 25 new insects become established in Hawaii each year. Of these accidental introductions, an average of three develop into pests of economic importance. Those achieving pest status do so because of Hawaii's lack of parasitoids and predators that had kept their populations at acceptable levels in their original home.

When a new insect pest is found in Hawaii, the PANIC (Planned Action for New Insect Control) committee, which is made up of entomologists from state, federal and private organizations (B. P. Bishop Museum, Hawaii State Department of Agriculture, Hawaii State Department of Health (Vector Control Branch), University of Hawaii, Hawaii Sugar Planters Association, U.S. Air Force, U.S. Army, U.S. Navy, USDA-ARS, and APHIS, etc.) meets and discusses a plan of action. A survey is made to determine the distribution of the insect while systematists confirm its identification. Spot treatments with a pesticide, such as malathion, may be used if warranted. Biological control has been our first line of defense since the late 1800's and continues to be the long-term goal for any new pest.

The tephritid fruit fly species, pests of economic importance in Hawaii, are the result of accidental introductions. Many people who live in Hawaii do not believe there is a problem with fruit flies. We have lived with the insects for so many years that we are used to them and have developed economical methods for control of the flies in our fruit trees and gardens. However, fruit flies in Hawaii are considered to be an export problem. Field control measures and commodity treatments have been developed by USDA-ARS and UH researchers to ensure that exported fruits and vegetables do not contain live tephritid eggs, larvae, pupae, or adults.

Four species of tephritid fruit flies have been accidentally introduced into Hawaii. In the time allotted to me I shall make brief remarks about each of the species in order of their appearance in our state.

The melon fly, *Dacus cucurbitae* Coquillett, arrived in Hawaii about 1895. It is the most important pest of vegetables in Hawaii (Back and Pemberton 1917). It has a wide host range and causes serious losses to crops such as melons, cucumbers, tomatoes, and especially other cucurbits. It has also infested

beans, peppers, papayas, and passion fruit. The host plant that carries populations through periods of scarcity of commercial crops is the weed, *Momordica balsamina* L. or wild bittermelon.

Gravid females will oviposit in the terminal shoots of host plants as well as small fruit. Under Hawaiian conditions it takes approximately 18-21 days for the melon fly to pass from the egg to the adult stage. Adults may live for several months. There is a preovipositional period of 8-10 days.

Foreign exploration in Malaya and India in 1915 led to the finding of *Opius fletcheri* Silvestri, a braconid wasp that parasitizes melon fly larvae. This larval parasitoid was released in 1916, and today it is more commonly recovered in melon fly infestations of wild momordica than in cultivated crops. The parasitoid averages about 17 percent parasitization of the melon fly. Other hosts for *O. fletcheri* include the medfly (Willard 1920). Parasitization of the melon fly is much greater in the wild momordica than the cultivated crops. Researchers believe there may be two melon fly populations, one in the wild host and another in the cultivated crops (Nishida and Bess 1957). The egg-larval parasitoid (*Biosteres arisanus*) of the medfly and oriental fruitfly also attacks melon fly eggs but cannot complete its development in them (Nishida and Haramoto 1953). Nishida (1955) reported four predators (ants, spiders, staphylinids, and reduviids) that attack the melon fly. The melon fly is partially controlled by these parasitoids and predators.

Prior to the development of the newer organic pesticides, mechanical control methods were the major means of reducing losses. Watermelon growers would wrap the melons (5 cm. diameter or larger) with newspaper. Approximately 30 days later the paper was removed and the fruits were exposed to sunlight for 48 hours to improve the color prior to harvest. Field sanitation (destruction of infested fruit) and fermenting lure traps were also used. University entomologists studied the ecology and control of the melon fly (Nishida and Bess 1957). Their studies revealed (a) the movement of newly emerged adults out of the cultivated fields into border vegetation, (b) diurnal movement of gravid females into and out of the crop areas, (c) the close association of the adults to certain non-host plants, and (d) the usually higher melon fly populations outside rather than inside the fields. Based on their research findings, today's farmers spray the plants (corn borders) with which the adults are associated rather than spraying the crop to be protected. Malathion, with or without protein bait, is the commonly used insecticide.

The USDA-ARS Tropical Fruit and Vegetable Research laboratory (Honolulu Fruit Fly Laboratory) developed mass rearing techniques of the melon fly for SIRM (sterile insect release method) and Cue-lure (4-(p-acetoxyphenyl)-2-butanone), a male

attractant, to monitor ports of entry and progress of sterile fly eradication programs.

Melon fly has been intercepted at mainland ports of entry by the federal inspectors 63 times (1973-1983) with one infestation developing in California. The cost of eradication in California was approximately $233,000.

The second accidental introduction to Hawaii was the Mediterranean fruit fly (medfly), *Ceratitis capitata* (Wiedemann), in 1910. Its host range includes over 250 fruits, vegetables, and nuts (Back and Pemberton 1918). It became wide-spread throughout Hawaii from sea level to 1,500 meters (4,927 feet). Today it is commonly found in host fruit at the higher elevations (above 600 meters (1,968 feet) due to competition from the oriental fruit fly.

The mean development time from egg to adult is approximately 19 days under optimum conditions. Adults may live two to three months or longer. Mating may occur two days after emergence. Females will oviposit in green as well as ripe fruit.

This introduction may be considered to mark the beginning of biological control of fruit flies. Nineteen species of natural enemies have been liberated in Hawaii for control of the medfly. Nine species have become established and an additional eight species purposely introduced for control of the oriental fruit fly also attack the medfly. Clausen (1956) reported that five species (*Opius humilis, B. tryoni, B. fullawayi, Dirhinus giffardii*, and *Tetrastichus giffardianus*) were established by 1914. Willard and Mason (1937) reported parasitization from 1914-1933 ranged from 24.9-55.8 percent with an average of 42.3 percent. *Biosteres (Opius) tryoni* has consistently been recovered from medfly. Today as high as 70 percent parasitization of mixed medfly and oriental fruit fly populations occurs. This is approximately the same level as reported by Haramoto and Bess in 1970.

USDA-ARS researchers have developed mass rearing techniques for SIRM (sterile insect release method) medfly eradication programs when mainland infestations occur. Their techniques for mass rearing of *B. tryoni* will be used in field tests to demonstrate if it is possible to suppress medfly populations with an inundation of parasitoids. They also developed the male attractant tri-medlure (t-butyl-4(or 5)-chloro-2-methyl cyclohexane carboxylate) that is widely used in surveys around ports of entry and to monitor progress in medfly SIRM programs. USDA-ARS laboratories have developed safe and economical commodity treatments, so that produce may be exported to the mainland.

University and USDA-ARS researchers are continuing basic

studies on medfly genetics and attractants. University researchers are participating in an international (BARD) cooperative agreement with medfly researchers in Israel (S. H. Saul, personal communication, 1985).

Most backyard gardeners pick their fruit and vegetables before it is stung and allow the fruit to ripen in the house. A few utilize the malathion bait sprays to protect their fruit trees from heavy losses. Medfly is not as abundant as the oriental fruit fly.

Between 1971-83 medfly has been intercepted 647 times (632 times from Hawaii) and four infestations have developed in California. The cost of eradication of these infestations was approximately $3,885,000 (R. V. Dowell, personal communication, 1985).

The third fruit fly introduction into Hawaii occurred in 1946 when the oriental fruit fly, *Dacus dorsalis* Hendel, was discovered infesting mangoes. This insect infests over 236 kinds of fruits, vegetables, and nuts. Wild guava, *Psidium guajava* L., which bears fruit throughout the year, is the major host which supports fly populations when commercial hosts are scarce.

Development from egg to adult may take as long as 19-22 days under optimum conditions. Gravid females may sting (oviposit) mature green as well as ripe fruit. Adults may live for two to three months or longer. Preovipositional period is 8-10 days.

Major explorations for natural enemies of tephritid fruit flies occurred after the discovery of oriental fruit fly (Van den Bosch and Haramoto 1951). Most of the tropical and subtropical areas of the world were explored, with special attention to Australia, China, India, Malaya, East, West and South Africa, and the Pacific Islands. Tephritid puparia were shipped to Hawaii and held in quarantine for emergence of the natural enemies and adult flies. Sixty species of tephritid fruit flies were reared from over 110 different kinds of fruit and 80 or more species of parasitoids were collected (Clausen 1956). Twenty-three species (16 larval, 6 pupal, and 1 predator) were liberated in Hawaii in 1947-1949. Several of the opiine species released at that time have recently been studied by systematists and declared synonyms of other species (Wharton and Gilstrap 1983). Today, eight of the thirteen species of natural enemies released have become established. Three of the imported species *Biosteres (=Opius) longicaudatus* Ashmead, *B. (=Opius) vandenboschi* (Fullaway), and *B. arisanus* (Sonan) *(=Opius oophilus* Fullaway) were the major contributors to biological control of the oriental fruit fly in Hawaii (Newell and Haramoto 1968; Haramoto and Bess 1970). Smaller larvae are parasitized by *B. vandenboschi*. Third instar larvae are parasitized by *B. longicaudatus*. The egg-larval parasitoid, *B. arisanus*, replaced the first two species in two

steps: (a) *B. vandenboschi* replaced *B. longicaudatus* as the key parasitoid in September 1949, and (b) the egg-larval parasitoid has outnumbered the other species of parasites since 1950. After 1951 *B. vandenboschi* and *B. longicaudatus* accounted for less than 5 percent of all parasites reared from guava. Today *B. arisanus (Opius oophilus)* is the key parasite for biological control of the oriental fruit fly and medfly. In mixed populations of oriental fruit flies and medflies at Kula, Maui (1978-1981), Wong et al. (1984) reported 80 percent of the parasitoids were *B. arisanus*. On occasion, *B. longicaudatus* and *B. tryoni* accounted for 32 and 8 percent of the parasitoids respectively. The egg-larval parasitoid, *B. arisanus*, also destroys melon fly eggs when it oviposits in them. The parasitoid cannot complete its development in the melon fly.

Several predators have been recorded attacking the eggs. larvae, pupae, and adults of the oriental fruit fly. Ants are general predators of the eggs and larvae in fruit that has fallen to the ground. Larvae leaving the fruit to pupate in the soil are most vulnerable to attack. Other insects attracted to ripe fruit on the ground also destroy eggs and larvae. Mice, birds, and other vertebrates may consume eggs and larvae when eating the fruit. Data on the importance of predators are limited.

USDA-ARS researchers have developed mass rearing techniques for SIRM eradication programs. They have devised male annihilation procedures utilizing methyl eugenol lures in traps or incorporated with thickening agents and dispersed by ground or aerial equipment. Mass-rearing techniques for the egg-larval parasitoid (*B. arisanus*) have been developed for use in field tests with inundation of parasites to suppress the oriental fruit fly populations. Investigations on the use of insect specific nematodes to suppress fruit flies emerging from the soil have shown some promise.

With the loss of ethylene dibromide as a fumigant for fresh produce to be exported to the mainland, alternative methods of fruit fly control that were acceptable to EPA had to be investigated. Couey et al. (1984) developed the double-hot water dip treatment of produce to be exported. According to H. M. Couey and C. Hayes (personal communication 1985), the improved treatment utilized papayas of 1/4 ripe or less (determined by the Hunter Colorimeter value of 23.4 at the stem end, or 27.4 at a yellow spot on the fruit) which are submerged in 41-43°C (105.8-109.4°F) hot water for 30 minutes and within 3 minutes transferred to 48-50°C (118.4-122.0°F) hot water for 20 minutes. Following the hot water treatment the fruit is rapidly cooled with water (20°C or 68°F) sprays. Some countries continue to accept fruit fumigated with ethylene dibromide. Malathion bait sprays developed by the USDA-ARS laboratory are used in oriental fruit fly population suppression.

University and State Department of Agriculture entomologists have studied and evaluated the parasitoids and predators introduced for control of oriental fruit flies. Since Miller et al (1983) reported methyl eugenol as being carcinogenic, investigations into compounds that may be replacements were initiated (Mitchell et al. 1985). This work is in cooperation with University of Illinois and USDA-ARS researchers. Phytoecdysones and insect growth regulators are being investigated as possible commodity treatments.

Research by Courtice and Drew and their colleagues (1983, 1984), studying the interrelationships and interactions between bacteria and tephritid species, has shown the importance of these organisms in the ecology of fruit flies. Their work has stimulated other research in this area. Further studies in Australia and Hawaii may lead to the development of more efficient and attractive lures, as well as environmentally acceptable control measures.

Most gardeners pick their fruit at a mature green stage of ripeness that is not attractive to ovipositing females. The fruit to be harvested may be bagged (paper bag) on the tree or taken into the house and allowed to ripen. Malathion bait sprays are applied by some growers. Methyl eugenol traps collect large numbers of males but are not very effective in controlling oriental fruit fly infestations. The oriental fruit fly is more numerous than medfly at the lower elevations.

Between 1971 and 1983, the oriental fruit fly has been intercepted 4,047 times, all from Hawaii, and 13 infestations have developed in California. Presently there are infestations in Sunnyvale and at Long Beach. The cost of eradication of the 12 previous infestations was approximately $817,000.

The fourth and most recent introduction was the solanaceous fruit fly, *Dacus latifrons* (Hendel), which was discovered in March 1983. It was intercepted by postal inspectors in California. Infestations are confined to the island of Oahu. This tephritid has been reported in China, Hawaii, India, Laos, Malaysia, Philippines, Taiwan, and Thailand but is not considered a pest of serious economic importance.

In Hawaii, Vargas and Nishida (1985) reported field infestations in egg plant, chili pepper, kikania-lei (*Solanum aculeatissimum*), the weed popolo berry (*S. nigrum* or *S. nodiflorum*), and tomato.

Entomologists of all agencies are assisting in developing information on the insect. The solanaceous fruit fly has not been attracted to any of the presently used fruit fly lures or to the experimental compounds tested. USDA-ARS personnel are trying to develop mass-rearing techniques for the fly. Biological and

ecological studies indicate the populations are low. One parasitoid, *Opius fletcheri*, has been recovered from puparia. The egg-larval parasitoid, *B. arisanus*, reported in the literature as attacking *S. latifrons*, has been recovered from mixed populations of oriental, mediterranean, and solanaceous fruit flies. The significance of this insect as a threat to agriculture in Hawaii or on the mainland is presently unknown.

In conclusion, the four tephritid fruit flies in Hawaii are not considered much of a problem to the citizens of our state, and those individuals involved in commercial fruit and vegetable host production have means for controlling these pests. Commodity treatments that are approved by EPA have been developed for produce that is to be exported. Hawaii provides a natural laboratory where research on all four species is possible at one location. Area control and eradication techniques have been developed and implemented to control or eliminate mainland infestations. There is partial biological control of oriental fruit fly and medfly in Hawaii. Biological control of the melon fly is poor, and no effective control measures have yet been developed for the solanaceous fruit fly.

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CHAPTER 3

Diapause Modalities in Some *Rhagoletis* Species

M. T. AliNiazee

Diapause is a physiological state of arrested development associated with cessation of morphological transformation and reduced biochemical activity, which enables insects to survive adverse environmental conditions. Diapause generally occurs in response to token stimuli (Lees 1955) and is expressed in some later stages of insect life. Insect seasonality in many respects reflects the adaptations of a given species to utilize environmental favorableness to quickly emerge, reproduce, and utilize the available resources and to cease activity as soon as the environmental conditions become unfavorable for continuation of those activities. Over time, insects have evolved to utilize changes in such important components of environment as temperature, photoperiod, rainfall, humidity, food quality, etc., and sometimes to utilize more subtle factors like disturbance, magnitude of fluctuation of an environmental factor, etc., to forecast oncoming of seasonal changes and to prepare accordingly (Saunders 1976, Beck 1980, Tauber *et al.* 1986). Thus diapause, which is primarily controlled by neurohormonal mechanisms, is an adaptive feature to seasonally predictable environmental changes. It shows a large degree of inter- and intra-species variations, and occurs at species-specific stage of life cycle; a single stage in most insect species.

The genus *Rhagoletis* comprises over 50 described species associated with diverse habitats. Most of the pest *Rhagoletis* feed on the pulp of growing fruit and cause substantial economic losses (Boller and Prokopy 1976, AliNiazee 1986a, 1986b). Most of the species belonging to the genus *Rhagoletis* are univoltine in nature. They emerge in early summer, complete one generation and enter into a diapausing stage during late summer and early fall, and stay in this pupal diapause for nearly 8-10 months before emerging as adults during the next year. The diapause characteristics in each species are different and have a direct bearing on the ability of an individual species to expand its geographic range of distribution and host race formation. For the sake of this discussion, I have attempted to analyze the diapause characteristics of three pest (*R. indifferens*, *R. pomonella*, and *R. completa*) and one non-pest (*R. zephyria*) species of *Rhagoletis* commonly found in the Pacific Northwest region of the United States.

Diapause in *Rhagoletis* can be divided into different distinct but overlapping phases. The course of diapause in

nature begins with a 'diapause induction phase,' the diapause is initiated in a 'diapause initiation and expression phase,' it continues in a 'diapause development phase,' it slowly ends in a 'diapause termination phase,' and is followed by a 'post-diapause development phase.' The dynamic stage of diapause is maintained during the 'diapause development phase' through the developmental or suppressive actions of a range of environmental factors including temperature and photoperiod.

A) Diapause Induction:

The diapause in *Rhagoletis* flies is induced by a complex interaction of genetic and environmental factors. In the case of the western cherry fruit fly, *R. indifferens,* for instance, the diapause is induced primarily through the engraved genetic mechanisms and seem to have little influence of various environmental factors. Maintenance of diapause-averting conditions such as long photoperiod and elevated temperatures have only marginal effects on diapause induction in this species. Data presented in Figure 1 show that less than 5 percent of the population in this species completed development without going into diapause when reared under non-diapause conditions. On the contrary, in the walnut husk fly, *R. completa,* and in the apple maggot, *R. pomonella,* over 75 percent of the population completed development in non-diapause conditions. Attempts to breed non-diapausing individuals by different cross breeding and back crosses suggest that in *R. indifferens,* the inheritance of diapause characteristics are probably governed by dominant genes.

The sensitivity of *Rhagoletis* flies studied in our laboratory varied considerably to diapause-averting conditions. Long photoperiods and elevated temperatures inhibited diapause induction in *R. pomonella* and *R. completa*, partially inhibited diapause in *R. zephyria*, and had relatively little effect on *R. indifferns* (Table 1). Prokopy (1968) also reported diapause aversion in a population of *R. pomonella* from Massachusetts. The diapause induction apparently occurs in the larval stage in those species where photoperiodic cues are used (AliNiazee, unpublished).

B. Diapause Initiation and Expression Phase:

The diapause is invariably expressed in *Rhagoletis* flies in the pupal stage. A series of dissection studies involving *R. indifferens* larvae (immediately after completion of larval stage) suggest that they were ready to express their diapause as soon as they matured. In case of *R. completa*, an abrupt change to long photoperiod at this stage had no effect on diapause aversion, which suggests that once diapause was induced, it was difficult to stop it. Similarly, once diapause was expressed, the length of photoperiod had no effect (AliNiazee, unpublished data) on the course of diapause.

Table 1. Relative proportion of the population entering diapause under diapause-averting conditions in some *Rhagoletis* species. Temperature 23 ± 1°C, 17:7 LD photoperiod.

Species	Host	% Entering diapause
R. indifferens	cherry	90 - 95
R. completa	walnut	10 - 30
R. zephyria	snowberry	25 - 45
R. pomonella	apple (Oregon)	15 - 45
	hawthorn (Oregon)	45 - 60

In *R. indifferns*, the early stages of diapause were maintained by elevated temperatures under field conditions. In the laboratory, sudden increase in surrounding temperature (after diapause was expressed) did not break the diapause and no distinct refractive phase (Mansingh 1971) was noticed. Similar behavior was noticed with *R. pomonella* pupae, although within a short period of time they were able to break the diapause and initiate post-diapause development in response to elevated temperatures.

The waiting period before the diapausing individuals are exposed to diapause development conditions in the field varies from species to species. In case of *R. indifferens* it could be anywhere between 60-90 days, while in case of *R. pomonella, R. completa,* and *R. zephyria* it may be only 15-30 days. Thus it is not surprising that they all respond differently to environmental cues at different stage of diapause. The evolutionary advantages for this differential response in terms of survival and exploitation of their environment are numerous. Perhaps one of the most important benefit is the synchronization of life cycle to utilize the available resources. In fact, this is the most significant aspect of diapause in many insect species (Danilevsky *et al.* 1970, Tauber and Tauber 1976, 1981).

Once diapause is initiated and expressed, it is maintained by elevated temperatures in *R. indifferns* and by declining photoperiods and moderately low temperatures (12-18°C) in *R. completa* and *R. pomonella* and *R. zephyria*. These modalities of diapause maintenance could vary from area to area depending upon the evolutionary changes occurring in these populations. It is inconceivable that a uniform mechanism occurs for all

populations of a given species throughout its distribution range.

C) Diapause Development Phase:

The term diapause development was originally proposed by Andrewartha (1952) to the stage where insects were reacting to cold temperatures and preparing themselves for post-diapause development. In most *Rhagoletis* flies, we denote this period to be from when they are ready to react to cold temperatures to when they are ready to respond to post-diapause development temperatures. As mentioned earlier, in case of *R. indifferens* it might take from 60 to 90 days before this phase begins after the initiation of diapause, and in other species it could be much shorter.

The length of cold temperature required for completion of diapause development phase varies from species to species and also depends on the severity of the cold (Table 2). In *R. indifferens*, Brown and AliNiazee (1977) showed that optimum diapause development occurred at 190-200 days when pupae were exposed to 3^{o}C. Later work by AliNiazee (unpublished) indicated that some compensation could occur and diapause development could be completed in 150-180 days, if slightly lower temperature (0^{o}C) and fluctuating temperatures were used during the diapause development phase. With *R. completa, R. pomonella,* and *R. zephyria,* diapause development completed at a slightly shorter period (110-120 days) and was similarly influenced by declining temperatures (AliNiazee, unpublished).

Heterogeneity was very common in this stage of diapause. Some individuals completed diapause development phase in less than 30 days (AliNiazee, unpublished, Brown and AliNiazee 1978), while others required as much as 200 days, and some required two to three winters before emerging as adults. The degree of this heterogeneity suggests genetic polymorphism in many *Rhagoletis* flies in their diapause response. This variation in diapause development affects post-diapause development and synchronization of emergence under field conditions.

Most *Rhagoletis* phenology models (AliNiazee 1976, 1979, Reissig *et al.* 1979, Laing and Heraty 1984) employ that a rather complete diapause development occurs in these flies during winter months and a uniform post-diapause development pattern occurs during the post-diapause development stage. This may be true in most of the distribution range of these flies; however, in areas where the optimum diapause development does not occur, a markedly different post-diapause development pattern could emerge, and should be taken into account while designing these models.

The heterogeneity of diapause development also has a marked effect on the distribution, host plant exploitation, host race formation, and geographic range extension of these flies. The

Table 2. Diapause and post-diapause development characteristics of some Rhagoletis flies.

Species	Diapause induction	Diapause maintenance	Diapause development	Diapause termination	Post-diapause development	In field non-diapause development
R. indifferens	Genetically controlled; little environmental influence.	Elevated temperature (>16°C). No effect of photoperiod.	Temp. optima: 0-9°C Range: -5-12°C Photoperiod: No effect.	Temperature dependent, low threshold 8.3°C. Photoperiod: No effect.	Temperature dependent optima: 16-24°C. Photoperiod: No effect.	None
R. completa	Genetically and environmentally controlled; relative values unknown.	Declining photoperiod and temperatures.	Temp. optima: 6-9°C. Range: -2-2°C. Photoperiod: Little or no effect.	Temperature dependent, low threshold 10.5°C. Photoperiod: Little or no effect.	Temperature dependent, optima: 20-28°C. Range: 12-35°C. Photoperiod: Little or no effect.	Occasional
R. pomonella	Genetically and environmentally controlled; photoperiod & temperature induced in larval stage.	Declining photoperiod and temperatures.	Temp. optima: 0-3°C. Range: -6-12°C. Photoperiod: Little or no effect.	Temperature dependent; low threshold 6.4-8.7°C. Photoperiod: Little or no effect.	Temperature dependent, optima: 18-24°C. Range: 10-32°C. Photoperiod: Little or no effect.	Rare
R. zephyria	Genetically and environmentally controlled; relative rates unknown; temperature & photoperiod induced.	Declining photoperiod and temperatures.	Temp. optima: 6-9°C. Range: -2-12°C. Photoperiod: Little or no effect.	Temperature dependent, low threshold 8.1°C. Photoperiod: Little or no effect.	Temperture dependent, optima: 16-22°C. Range: 10-32°C. Photoperiod: Little or no effect.	Rare

fringe populations (those showing extremes in diapause development response) could survive and establish new populations and get isolated due to sympatry or allopatry, and eventually develop different biological traits.

D) Diapause Termination Phase:

In most *Rhagoletis* flies this appears to be a very short duration of time and is generally an overlapping period between the diapause development and post-diapause development phases. However, under field conditions the diapause termination occurs slowly over a period of 4-8 weeks. In the diapause termination phase the insects are physiologically very active, go through various biochemical processes, and become ready to respond immediately to post-diapause development cues. Under field conditions these cues are characterized by moderating temperatures and slowly extending photoperiods. In *R. indifferns*, the post-diapause development is rapid if the pupae are passed through a 1-2 week period of moderate temperatures (12-16^{o}C) versus directly exposing them to normal development temperatures (20-24^{o}C). Such data are not available for other *Rhagoletis* flies. Again a heterogenous response was noticed in terms of length of this stage in different individuals of a given population. This may represent a continuation of heterogeneity of 'diapause development stage.'

E) Post-Diapause Development Phase:

The post-diapause development phase has been distinguished from the other phases of diapause by characterization of an immediate development response when the environmental conditions become suitable, resulting in morphological and physiological changes.

The post-diapause development occurs above a certain temperature threshold (zero developmental threshold) and generally only after the diapause development has been completed. The post-diapause development threshold may fluc- tuate slightly over the entire developmental period, although this has not been well documented in *Rhagoletis* species. The speed of post-diapause development is directly dependent upon the magnitude and intensity of diapause development and the acceleration of temperatures during the post-diapause development phase. The length of photoperiod appears to have little effect during the post-diapause development phase in *Rhagoletis*. For instance, in *R. indifferns* the time to adult emergence after 180 days of cold at 3^{o}C exposure was approximately the same for two sets of pupae, one placed in constant light and the other in constant dark.

The post-diapause developmental thresholds have been determined for a number of species of *Rhagoletis* by experimental analysis. For instance, van Kirk and AliNiazee (1981) determined

that the lower developmental threshold varies slightly depending upon the method of calculation. However, a generalized threshold of 8.3°C was suggested for this species. Similarly, Stark and AliNiazee (1982) modeled the post-diapause development of this insect and presented a linear functional response between 12 and 25°C, a declining developmental response from 25 to 30°C, and a lethal response above 30°C. This type of data are not available for other *Rhagoletis* species.

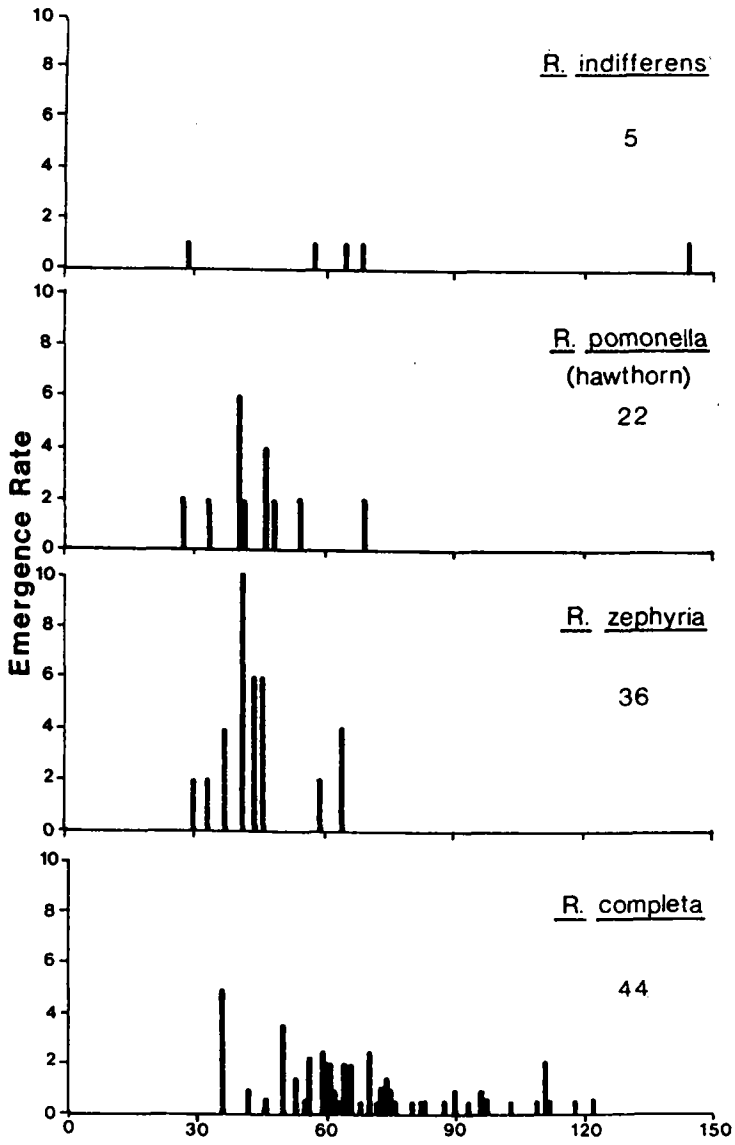
Attempts have been made to model the post-diapause development of two *Rhagoletis* species for prediction of adult emergence using a thermal summation scale (AliNiazee 1976, 1979, Reissig *et al.* 1979, Laing and Heraty 1984). A lower developmental threshold of 8.7°C was determined for *R. pomonella* from Ontario (Keith and Laing 1978), and a threshold of 6.4°C from New York (Reissig *et al.* 1979). Variation of this threshold (± 5°C) apparently had little influence on the accuracy of prediction of apple maggot emergence.

It should be noted that the post-diapause development synchrony is dependent upon the homogeneity of the completion of earlier diapause development and termination stages. The transitory diapause completion and termination phase may require a different 'temperature optima' than either the diapause development or post-diapause development phases. The length of photoperiod generally seems to have no influence during these phases, but further investigations are required to determine the real impact of this factor. However, a more uniform development of pupae and adult emergence occurs when the insects are exposed to optimum diapause development conditions.

The role of other environmental factors, including humidity and rainfall, has not been investigated in detail. It is obvious that some of these factors will have an impact in some *Rhagoletis* species.

The lack of responsiveness of some individuals (5-15 percent) in *Rhagoletis* species studied to post-diapause development temperatures, and the tendency to stay in diapause for more than one year or as long as 3-4 years, suggests that an overriding mechanism exists, perhaps mainly controlled by genetic traits. The proportion of population that stays more than one year in diapause probably varies from species to species and from year to year. The severity of cold temperatures during the diapause development phase and the pattern of temperature dynamics may also be responsible for this prolonged diapause.

Genetically controlled heterogenous response to diapause and post-diapause development perhaps is the most important survival mechanism in *Rhagoletis* species. Partial non-diapause development as noticed in some *Rhagoletis* species (Figure 1) is



Non-diapause emergence of some Rhagoletis flies

Figure 1. Emergence (number out of 100) of adult flies under diapause-averting conditions. Nearly 50% of the remaining pupae were parasitized.

also an important synchronizing and survival mechanism. Considering the evolutionary basis of native host fruit exploitation, it is not surprising that these diapause patterns exist. For example, the native host plants of *R. indifferens* in the western United States, such as *Prunus emarginata*, are alternate bearers. A very small amount of fruit is produced during certain years, which may not be enough to sustain even a small population of *R. indiffernes* larvae. This would cause a large mortality and perhaps extinction of this species. Thus the heterogenous diapause response serves as an insurance policy providing protection under adverse conditions. Similar situations may exist with other *Rhagoletis* species.

F) Classification of *Rhagoletis* Based on Diapause Modalities:

A close examination of the diapause behavior of the species studied (*R. indifferens, R. pomonella, R. zephyria,* and *R. completa*) suggests that distinct differences exist among them. For example, *R. indifferns* has a rigid diapause, where diapause induction is entirely controlled by genetic traits with relatively little impact of exogenous environmental factors, which is classified as a 'unimodal' diapause response. On the contrary, *R. pomonella* can be averted from going into diapause by the manipulation of environmental factors during larval stages. Higher temperature (>25^{o}C) and prolonged photoperiod (>18 hours) eliminate diapause induction in a large proportion of population in *R. pomonella* (Prokopy 1968, Mohammad and AliNiazee, unpublished). Some populations of *R. pomonella* from hawthorn host are much more restricted in their diapause requirements than the populations from apple. I am calling this a 'bimodal' diapause response. *R. zephyria*, like *R. pomonella* from apple, seems to provide an intermediate response to environmental manipulation, where >50 percent of the individuals will avert diapause under diapause-averting conditions. *R. completa*, on the other hand, seems to be the most diverse *Rhagoletis* species in terms of diapause. It represents what I call a 'polymodal' diapause response (Table 3), where different populations express different types of diapause patterns. Further studies with other species of *Rhagoletis* are required to broaden this classification.

The nature of diapause may explain the potential of these species in expanding the distribution range and formation of new host races. *R. indifferns* and *R. fausta* are good examples of 'rigid diapause' insects. The distribution of *R. indifferns* is limited only to the Pacific Northwest, parts of Utah, and only to the higher elevations of northern California. This species failed to survive the lower valley conditions of California, although it was introduced to that area repeatedly. Similarly, the 'intermediate flexible diapause' species, *R. zephyria,* also has a limited distribution, even though its host plant is found in parts of California. *R. pomonella*, on the other hand, has a wider distribution range (Bush 1966, AliNiazee and Brunner 1986),

and seems to adapt to new hosts in some western states. *R. completa* seems to be the most flexible of *Rhagoletis* species studied. It is found from northern Mexico to British Columbia.

Table 3. Classification of *Rhagoletis* species based on diapause characteristics.

Suggested group and species involved	Diapause Development Modality	
	Flexibility of diapause induction requirements	Flexibility of diapause development requirements
Unimodal *R. indifferens* *R. fausta* ? *R. cingulata* ?	Narrow: genetically controlled, little environmental influence, can be averted in <5% of the population.	Narrow: chilling essential.
Bimodal Type A. *R. pomonella* (hawthorn)	Moderately flexible: controlled by genetic traits and environmental factors, can be averted in ca. 50% of the population.	Moderate: chilling is helpful but not essential. Diverse response to chilling conditions.
Type B. *R. pomonella* (apple) *R. zephyria*	Flexible: highly influenced by environmental cues, can be averted in >50% of the population.	Moderately high: chilling helpful. A wide range of temperatures in which diapause development may occur.
Polymodal *R. completa*	Highly flexible: mainly influenced by environmental factors, can be averted in nearly all of the population. A large degree of polymorphism in diapause response in different populations.	High: chilling is not required.

Summary and Conclusions

Diapause in *Rhagoletis* is a complex response to seasonal changes in the environment. Among the species studied, some show a more flexible response to diapause inducing and terminating environmental factors than the others. Diapause is maintained by elevated temperature in some species and by moderately declining temperature in others. Diapause development 'temperature optima' as well as the 'post-diapause development threshold' varies from species to species slightly. *R. indifferns* is the most 'rigid' species in its diapause induction response, while *R. completa* appears to be the most flexible. An understanding of diapause in *Rhagoletis* could serve an important purpose in the development of useful information regarding their distribution, geographic range extension, and host race formation. Such understanding is also very useful in developing predictive models and decision support system models for use in integrated pest management programs.

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CHAPTER 4

Divergence in Key Host Examining and Acceptance Behaviors of the Sibling Species *Rhagoletis mendax* and *R. pomonella* (Diptera: Tephritidae)

Todd J. Bierbaum and Guy L. Bush

Host-associated races and species of phytophagous insects provide an opportunity to address fundamental behavioral and evolutionary problems concerning natural selection and the evolution of reproductive isolation. Several plant protection programs have also focused on insect biotypes during their efforts to increase insect resistance in major crop plants (e.g., Gallun 1977; Gallun and Khush 1980; Sogawa 1982). Unfortunately, behavioral and life-history traits causing differences in the host plant specialization of insect species are poorly understood at both the genetic and phenotypic levels. Through studying these traits, we hope to gain insights into the biological mechanisms governing the evolution of host-associated races and species. In this paper we focus on a field study of the host examining and acceptance behaviors (sensu Miller and Strickler 1984) of two sibling species of *Rhagoletis* fruit flies.

One of the species, *R. mendax,* occurs in the eastern United States and Canada infesting the fruits of high and low bush blueberries *(Vaccinium corymbosum* and *V. angustifolium)*, and a few representatives of the genus *Gaylussacia* (Ericaceae). The second species, *R. pomonella,* infests apple *(Malus* sp.), hawthorne (*Crataegus* sp.), rose hips (*Rosa rugosa*), sour cherries (*Prunus cerasus* L.), and occasionally other plants distributed among six genera of the Rosaceae in the United States, Canada, and Mexico (Bush 1966; Shervis et al. 1970; Prokopy and Bush 1972; Prokopy and Berlocher 1980). Independent lines of evidence based on chromosomal, morphological, and electrophoretic data (Bush 1966; Berlocher and Bush 1982) indicate *mendax* and *pomonella* are two of the most closely related species within the *pomonella* group. Although there is a high level of genetic similarity between the species, they have consistent differences in morphological (Curran 1932; Bush 1966), electrophoretic (Berlocher 1980; Berlocher and Bush 1982), life-history, and behavioral traits (Bierbaum and Bush 1988). The genetic similarity between these species has allowed us to hybridize them in the laboratory, and rear interspecific hybrid larvae in apples and blueberries under natural conditions in the field (Bierbaum and Bush 1988). This enables a genetic analysis of life-history and behavioral traits differentiating these closely related species.

From a theoretical standpoint, the formation of host races appears to be an important step in the development of new species of phytophagous insects (Bush 1974; 1975a; Bush and Diehl 1982). This topic has been of long-standing interest to evolutionary biologists and has been extensively debated (Mayr 1963; Bush 1969; 1975b; Bush and Howard 1986; Futuyma and Mayer 1980; Futuyma 1983; Jaenike 1981; Felsenstein 1981; Rice 1984). Theoritical analyses have shown that the formation of host races can be facilitated when mating occurs on the host plant (Bush 1975a; Rice 1984); under these conditions mate and host selection are closely linked in the behavioral repertoire and host selection can serve as a major mechanism to restrict gene flow between populations. Theories have also postulated that the evolution of a new host-associated species often involves genetic changes in at least two major components of the insect's genome. First, the adults need to acquire the ability to preferentially find and accept a new host for oviposition and in some cases mating, and second, the larvae must be able to survive on the new host (Bush 1975a; Bush and Diehl 1982). Population genetic models (Felenstein 1981; Rice 1984) have explored various mechanisms of host race formation and speciation, and have shown how fitness differences in alternate habitats and the level of habitat-based assortative mating can influence the evolution of reproductive isolation. Their results indicate the importance of data on host selection and survival abilities in understanding the formation of host-associated species.

Although a few empirical studies have ascertained genetic differences in the viabilities and host acceptance behaviors of closely related races and species of phytophagous insects (e.g., Hatchett and Gallun 1970; Huettel and Bush 1972; Knerer and Atwood 1972; 1973; Phillips and Barnes 1975; Carson and Ohta 1981; Bierbaum and Bush 1988), there is relatively little information on the phenotypic and genetic bases of these important traits (for reviews see Diehl and Bush 1984; Futuyma and Peterson 1985). In field experiments we have tested for differences in the host acceptance behaviors and larval-to-adult survival rates of *mendax* and *pomonella* flies on apple and blueberry plants. In this paper we focus on the results of behavioral experiments designed to test if the species differ in: i) the percentage of females ovipositing in apple and blueberry fruits, ii) the total number of eggs laid in each host fruit, and iii) number of occurrences, sequence, and duration of the host examining and acceptance behaviors preceding and following oviposition. We have identified key behavioral differences between *mendax* and *pomonella* that will serve as a basis for further genetic analyses.

MATERIALS AND METHODS

To record the number of occurrences, sequence, and duration of 14 host examining and acceptance behaviors displayed by mated

females, we developed a BASIC language Behavioral Sequence Recording Program for a TRS-80, model 100 portable microcomputer (Tandy Corporation, Fort Worth, Texas). The duration of the behavioral events was recorded with an accuracy of 1.0 seconds. Each plant was subdivided into bottom, middle, and top regions of the fruits, leaves, and branches in order to record the position of the released insect. This resulted in 126 behavior and plant location combinations that could be recorded by pressing single keys on the computer keyboard. A behavioral display was counted as a new occurrence if it was preceded by a different behavior or it occurred in a new plant position (e.g., bottom, middle, or top regions of the fruit). During releases of several mated females to blueberry and apple plants, we made videotape records of their behavior using a GP-5A Hitachi color video camera with a Schneider-Kreuznach macro- telephoto lens. These video records helped to detail several behaviors that were incorporated into the computer program for collecting the quantitative field observations.

We worked with mature (18 to 25 day-old) mated *pomonella* females obtained near Hart, MI, and *mendax* from Sawyer, MI. The flies were reared from pupae collected the previous summer and chilled at 4°C for six months, then incubated at 25°C with a 15L:9D photoperiod. Adults were held in 15 cm x 15 cm x 15 cm wire screen and plexiglass cages at a density of 10 females and 5 males, and were reared to maturity on a standard yeast hydrolysate and brown sugar diet (Prokopy and Boller 1970). The females were naive in the sense of not being exposed to either blueberry or apple plants prior to their testing in the field.

On the first day of each observation, a single female was released to the fruit of one of the two host plants and her behavior was recorded. She was then taken to the lab and held in a constant temperature chamber at 25°C for one day; on the third day, she was brought back to the field and released to the alternative host plant. One half of the test group was released to blueberries first, and the second half was released first to apples. The behavior of each fly was recorded until: i) it flew off the plant to the ceiling or sides of the field cage or ii) 20 minutes had elapsed. We completed a total of 166 female releases to blueberries and apples; 82 of these observations were *pomonella* flies and 84 were *mendax* flies.

Plants for each observation were kept inside a 3m x 2m x 2m clear saran plastic mesh cage in an abandoned field adjacent to a wooded nature preserve on the MSU campus. We used a potted 2.4m high apple tree and a 1.2m blueberry bush with fruits wired to their branches immediately prior to the release of a female. The fruits were free of pesticides and were harvested one day before their use; they were protected in the field from insect infestation by nylon mesh bags covering the branches of plants. Prior to the observations on each female, five McIntosh apples were

wired to the apple tree and a set of five clusters of Bluehaven blueberry fruits (with three ripe fruits per cluster) were attached to the blueberry bush. The fruits were placed in the same marked locations on the host plants for each release.

Data files were stored in the laboratory on computer disks at the end of each day of observations. Records in the files consisted of numerical and alphabetical codes specifying a behavior, location on the plant, and starting and finishing times of the behavioral display. The number of occurrences and duration time of behaviors displayed by an individual female at different plant locations, and the total time (residence time) on the fruits, leaves, and branches were calculated from the records. The following results focus on five behaviors that were closely linked with the act of oviposition into a fruit. The results for additional behaviors and plant locations will be reported elsewhere.

RESULTS

Residence Times on Fruits, Leaves, and Branches

Figure 1A gives the distributions of the total time spent by individual *mendax* and *pomonella* females on apple fruits. The time spent by *pomonella* females on apples was almost three times the mean residence time for *mendax* flies. The *mendax* distribution was skewed in the direction of individuals that spent short periods of time (less than 200 seconds) on apple fruits. *R. pomonella* females showed a broader range of residence times on apples than *mendax*. The distributions for most of the behaviors we analyzed do not match a normal probability function, and therefore we used nonparametric statistics to analyze our data. Using the Mann-Whitney U-test (Sokal and Rohlf 1981), the distributions of the time spent by *mendax* and *pomonella* females on apples are significantly different ($U(s)=1454.0$, $P<0.01$).

A large number of *mendax* females did not alight on the leaves of the apple plant (see zero histogram bar for the *mendax* distribution in Figure 1B), but over half the *pomonella* flies spent greater than 75 seconds on apple leaves. This resulted in a four-fold longer residence time for *pomonella* compared to *mendax* (Figure 1B, $U(s)=1295.0$, $P<0.01$).

There was a different pattern to the time spent by the same females on blueberries. Although there was no significant difference between *mendax* and *pomonella* in the length of time spent on blueberry leaves (Figure 2B, $U(s)=909.5$, $P>0.2$), differences occurred for the total time spent on blueberry fruits (Figure 2A, $U(s)=1069.5$, $P<0.05$). The longer mean residence time of *mendax* females on these fruits was due to a larger fraction of females that engaged in preovipositional, ovipositional, and postovipositional behaviors.

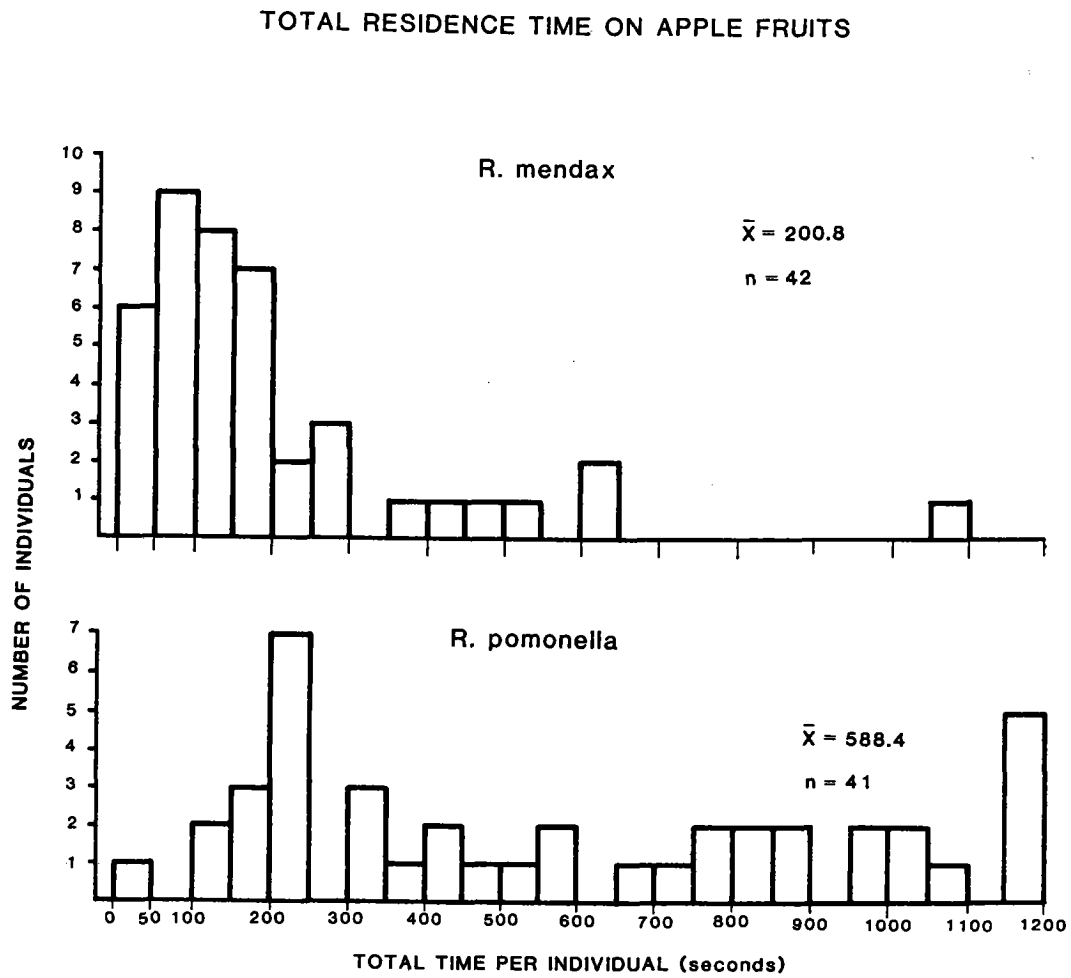

Figure 1A. Total time spent by *R. mendax* and *R. pomonella* females on apple fruits during 20-minute obervation periods.

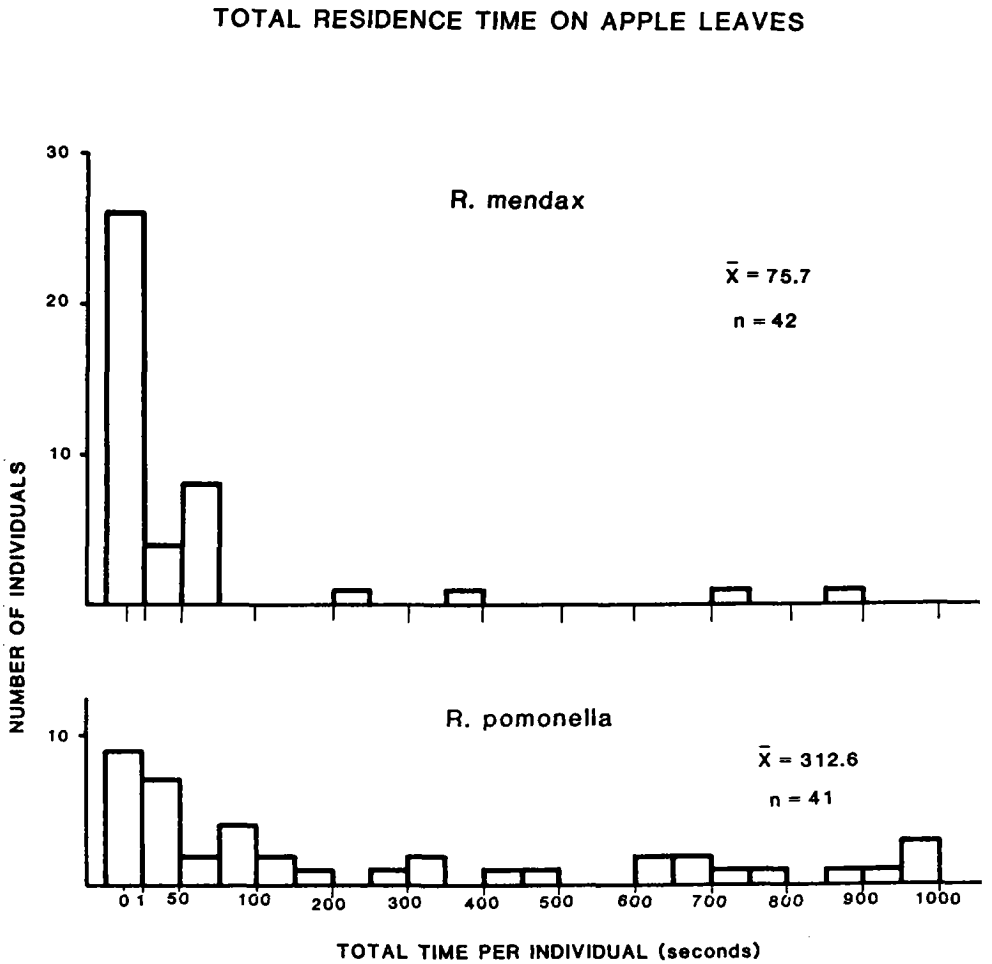

Figure 1B. Total time spent by *R. mendax* and *R. pomonella* females on apple leaves during 20-minute observation periods.

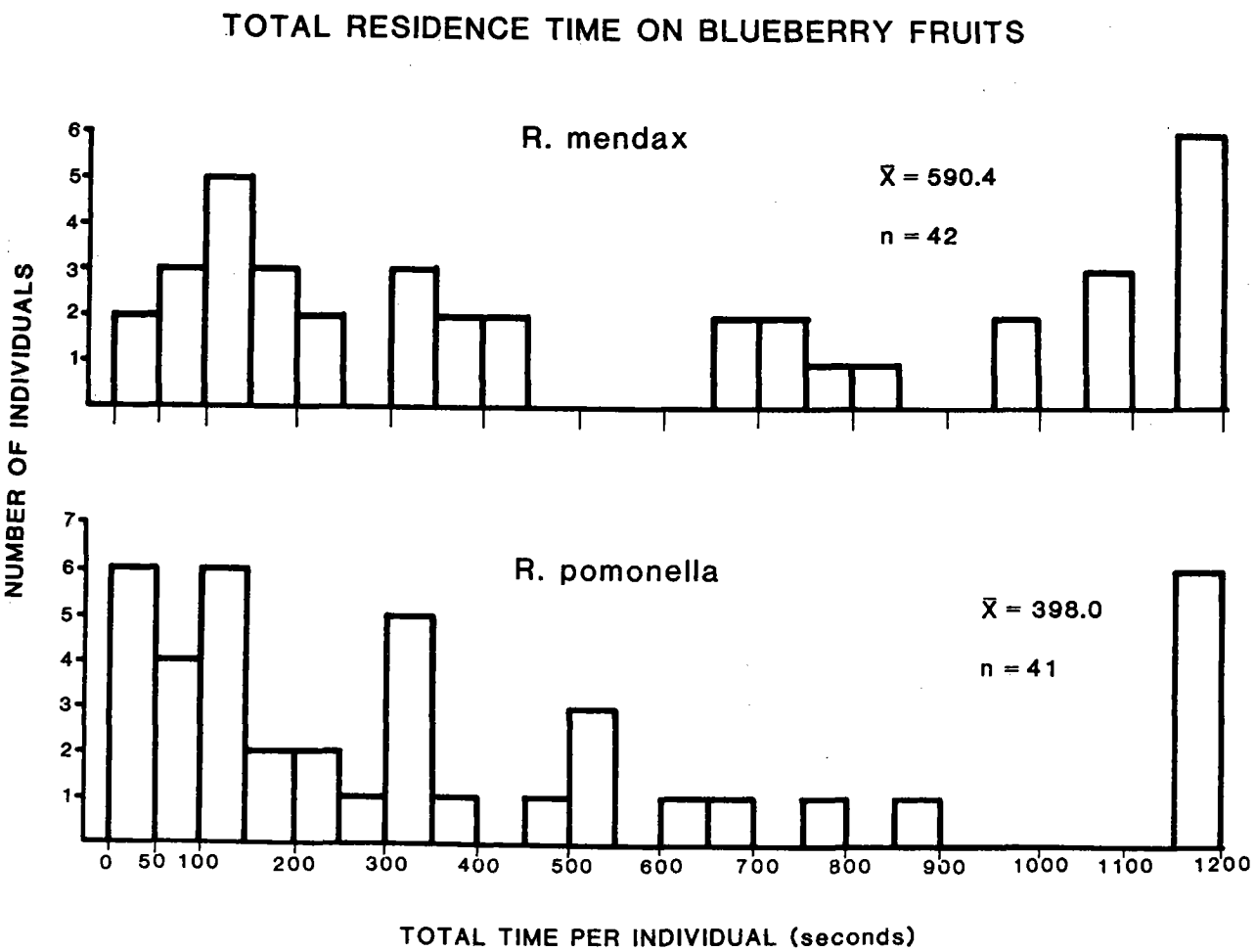

Figure 2A. Total time spent by *R. mendax* and *R. pomonella* females on blueberry fruits during 20-minute observation periods.

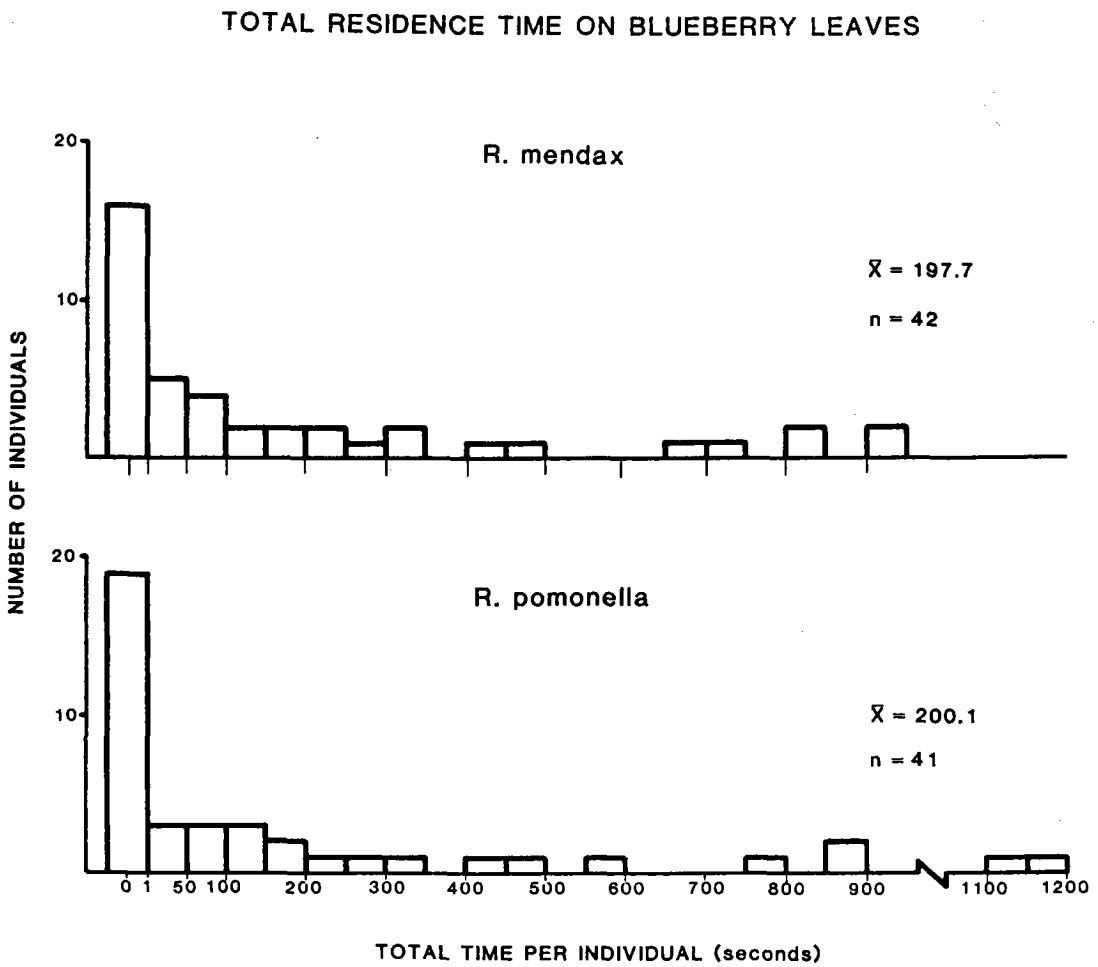

Figure 2B. Total time spent by *R. mendax* and *R. pomonella* females on blueberry leaves during 20-minute observation periods.

The total residence time on branches of both host plants was small compared to the residence times on either fruits or leaves, and comparisons between the species did not show differences in the amount of time they spent on either blueberry ($U(s)=905.5$, $P>0.1$) or apple ($U(s)=911.5$, $P>0.1$) branches.

Host Examining and Acceptance Behaviors Displayed on Fruits

The following focuses on several host acceptance behaviors strongly associated with ovipositing into blueberry and apple fruits. Prior to bending her abdomen for oviposition, a female walked with her head tilted towards the fruit with the labellum of her mouthparts periodically touching the surface (lapping) (i.e., she touched the surface of the fruit, then raised her mouthparts, and repeated the behavior). On a few occasions, a female also touched the surface of the fruit with the tip of her third antennal segment (antennating). Following either lapping or antennating, she turned approximately 180 degrees, bent her abdomen and probed the fruit with her ovipositor. Probing the fruit is often (but not always) followed by the insertion of an egg into the puncture. After an egg was laid, the female began dragging her ovipositor over the surface of the fruit. During this behavior, she emitted a marking pheromone that partially deterred other females from laying an egg in the same fruit. (Prokopy 1972; Boller 1981; Boller and Hurter 1985).

The species showed differences in the number of occurrences of the lapping behavior on apples. *R. mendax* females displayed this behavior less often than *pomonella* females (Figure 3A, $U(s)=1149.5$, $P<0.01$; 55 percent of the *mendax* females did not display the behavior compared to 27 percent of the *pomonella* flies). In contrast, *mendax* females touched the surface of blueberry fruits with their labellum a greater number of times than *pomonella* females (Figure 3B, $U(s)=1207.0$, $P<0.01$).

Antennating was a relatively rare behavior, but differences existed between the species in the number of antennal contacts with both blueberry and apple fruits. On apples, the mean number of antennal contacts per *pomonella* female was 35 times the value for *mendax* (Figure 4A, $U(s)=1032.0$, $P<0.01$). On blueberries, the reverse occurred with *mendax* females displaying 14-fold more antennating than *pomonella* (Figure 4B, $U(s)=967.0$, $P<0.05$).

R. mendax and *R. pomonella* showed pronounced differences in the number of ovipositor probes into apple fruits (Figure 5A, $U(s)=1155$, $P<0.01$). None of the 42 *mendax* females probed apples with their ovipositor, whereas *pomonella* females probed apples from 0 to 9 times, with a mean of 1.2. *R. pomonella* females often probed an apple fruit for several brief periods prior to oviposition. This exploratory probing and the previously described lapping and antennating behaviors probably provided essential sensory information stimulating a female to either

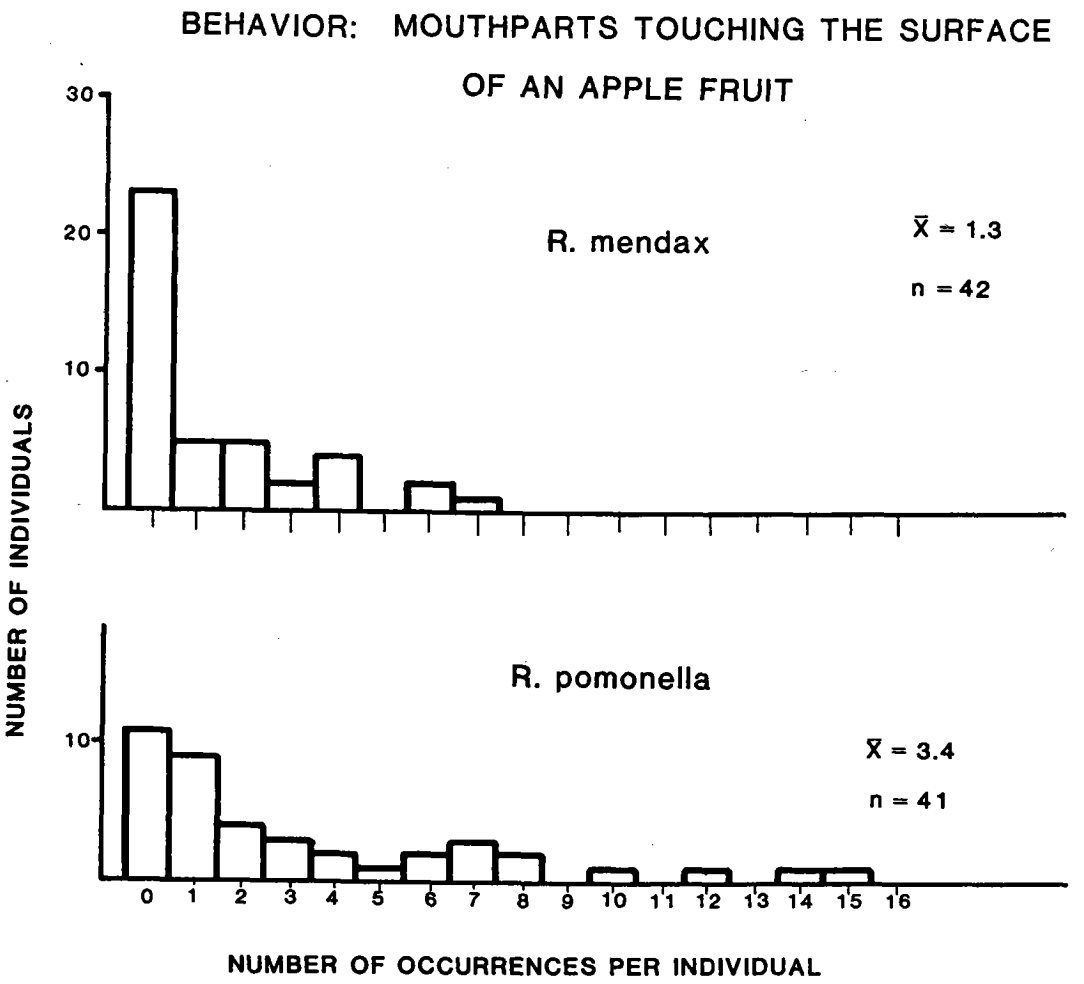

Figure 3A. Number of occurrences of the lapping behavior by *R. mendax* and *R. pomonella* females on apple fruits.

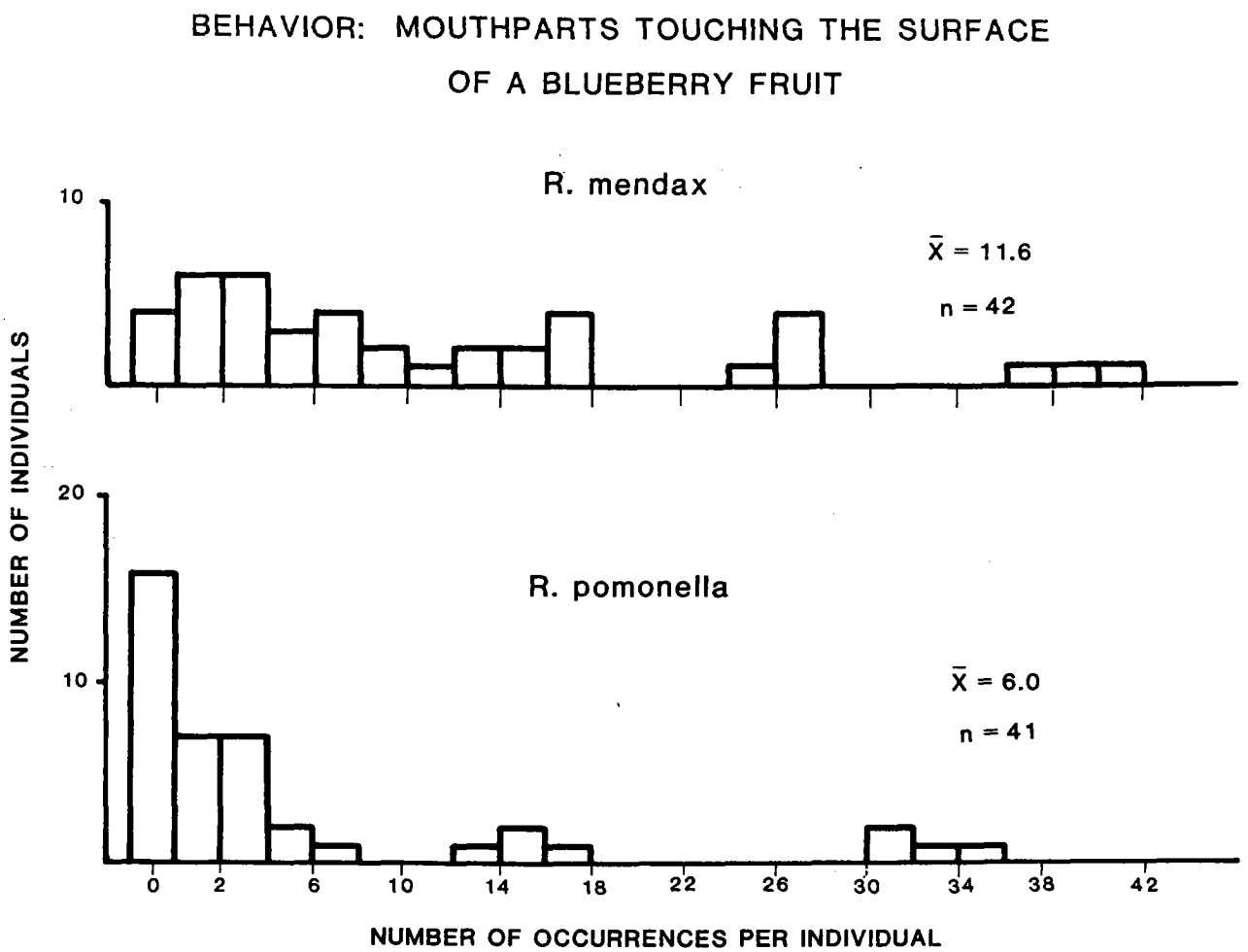

Figure 3B. Number of occurrences of the lapping behavior by *R. mendax* and *R. pomonella* females on blueberry fruits.

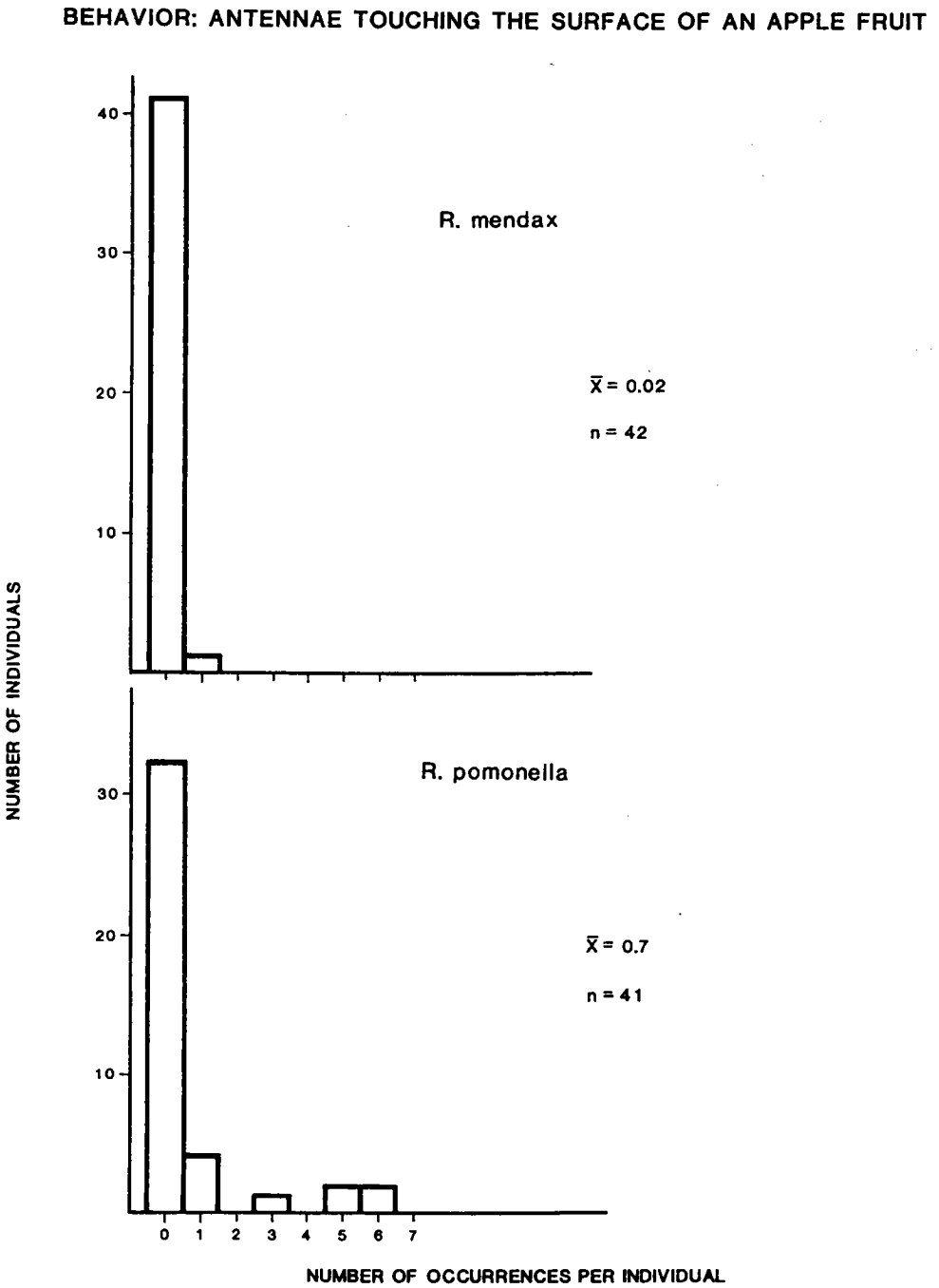

Figure 4A. Number of occurrences of the antennating behavior by *R. mendax* and *R. pomonella* females on apple fruits.

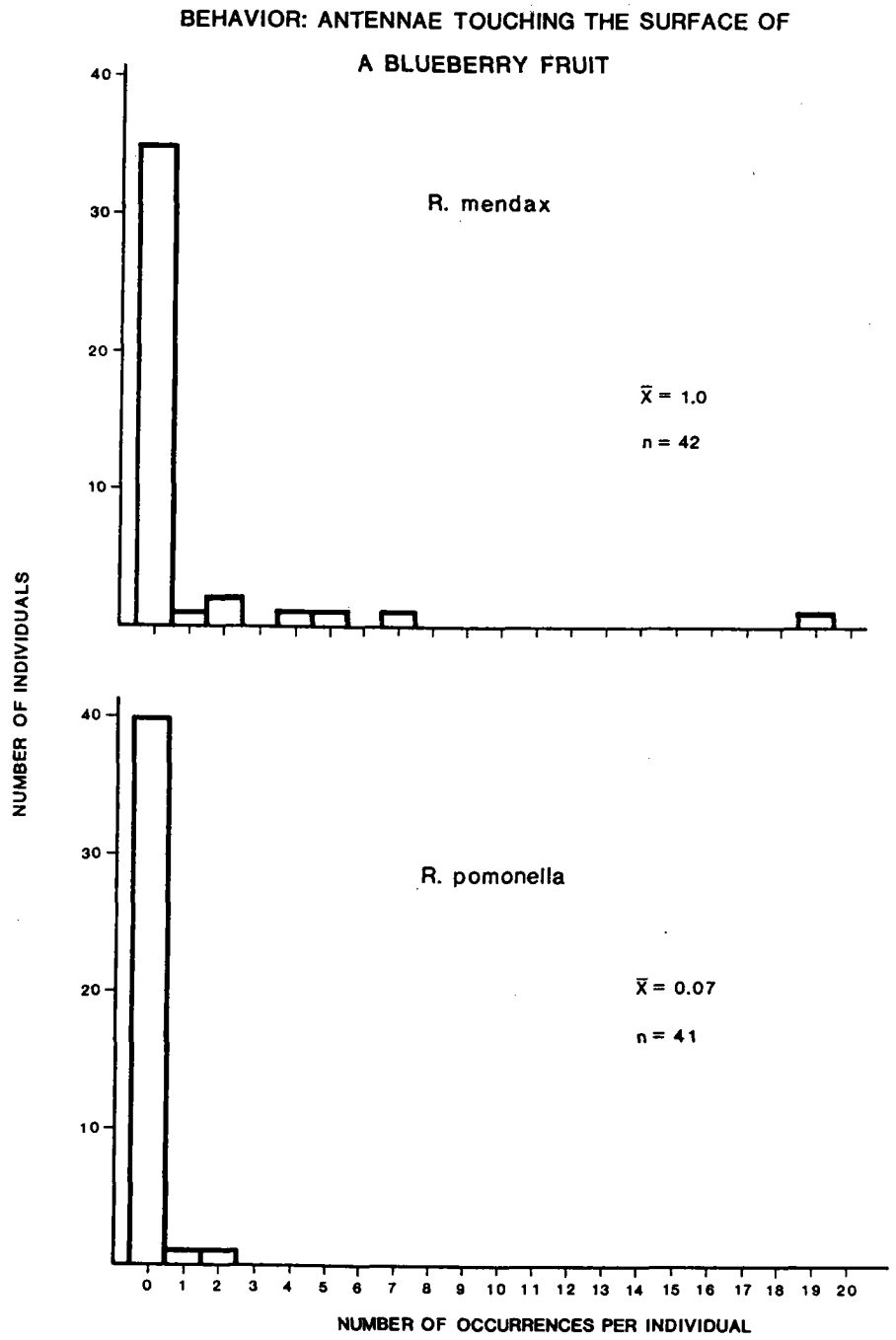

Figure 4B. Number of occurrences of the antennating behavior by *R. mendax* and *R. pomonella* females on blueberry fruits.

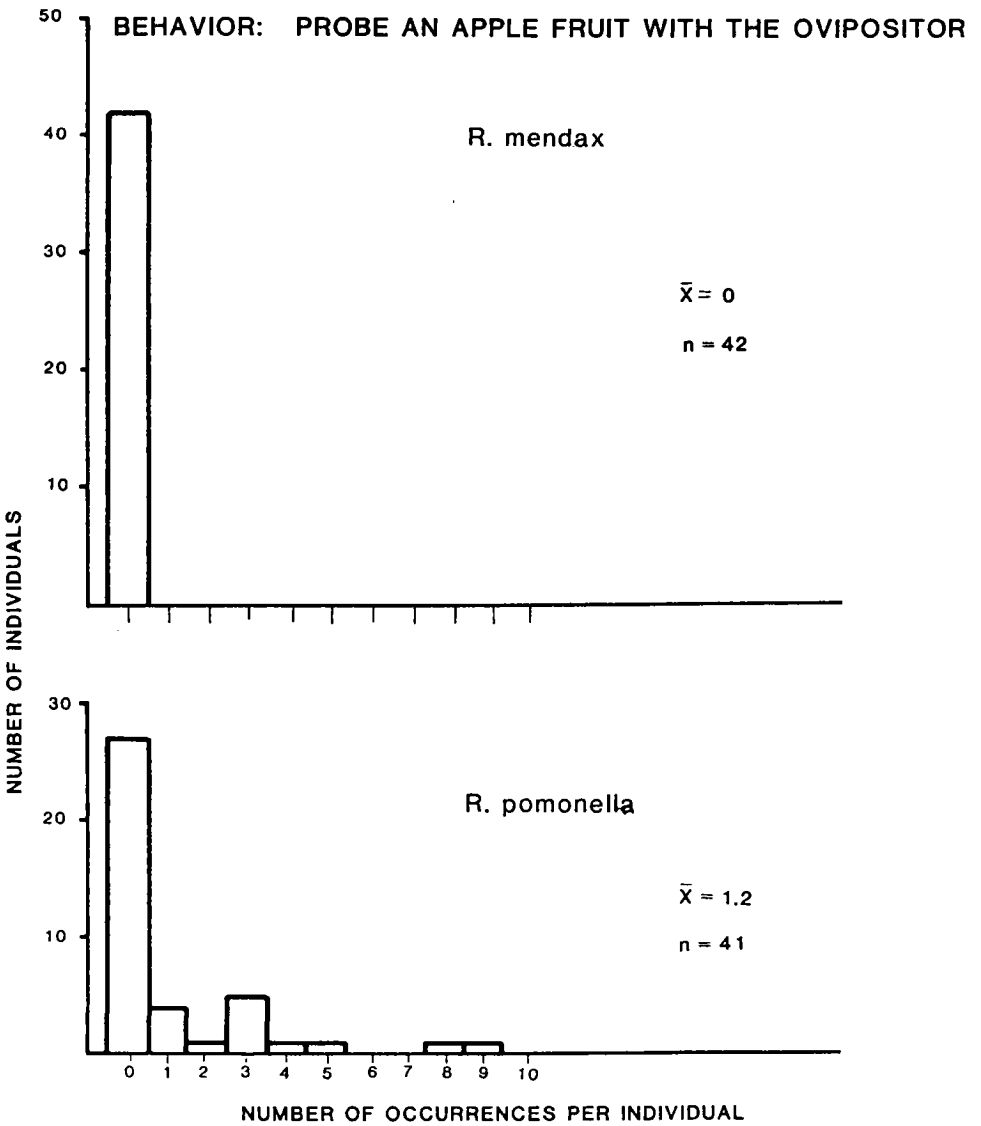

Figure 5A. Number of occurrences of the probing behavior by *R. mendax* and *R. pomonella* females on apple fruits.

oviposit or depart from the fruit.

A different pattern of ovipositional probes was observed on blueberry fruits; several *mendax* females rejected apple fruits but accepted blueberries. This alteration of behavior resulted in a four-fold greater mean number of probes in blueberries by *mendax* females compared to *pomonella* females (Figure 5B, $U(s)=1209.5$, $P<0.01$).

The differences in the preovipositional behaviors of *mendax* and *pomonella* were correlated with differences in the percentage of females that laid at least one egg into a fruit. Individuals initiating more preovipositional behaviors had a higher chance of laying an egg in the fruit. We refer to a female that lays one or more eggs per 20-minute observation period as an acceptor. On blueberries, the percentage of *mendax* acceptors was significantly higher than the percentage of *pomonella* acceptors, and the reverse pattern was observed on apples. Unexpectedly, the percentage of *pomonella* females ovipositing in blueberries did not differ significantly from the fraction ovipositing in apples (Table 1).

The two species also differed in the number of eggs laid per female in apples and blueberries. When averaged over accepting and nonaccepting females, *mendax* flies laid an average of 1.7 eggs in blueberries compared to 0.4 eggs per *pomonella* female ($F=15.7$, $P<0.01$). No *mendax* females accepted apples, and *pomonella* flies had significantly higher rates of oviposition (0.3 eggs per female) into this fruit ($F=13.7$, $P<0.01$).

The differences in rates of egg laying were linked with differences in the occurrence of ovipositor dragging on each host fruit. The *pomonella* females initiated a greater number of drags on the surface of apple fruits (Figure 6A, $U(s)=990.5$, $P<0.01$) compared to *mendax* females. The opposite relationship held on blueberries where *mendax* females invested all their eggs (Figure 6B, $U(s)=1202.5$, $P<0.01$).

Lastly, the two species differed in the amount of time spent in specific grooming behaviors on each host fruit. After dragging, both species preened the ovipositor with hind tarsi. This behavior was displayed primarily on fruits, and rarely occurred on either branches or leaves. On blueberries, *mendax* females spent a greater period of time preening their ovipositor compared to *pomonella* females (Figure 7A, $U(s)=1247.5$, $P<0.01$), and the differences between the species were again reversed on apples (Figure 7B, $U(s)=1206.0$, $P<0.01$).

DISCUSSION

R. mendax and *R. pomonella* have diverged in several key host examining and acceptance behaviors. The lack of probing and

Table 1. The percentage of *R. mendax* and *R. pomonella* females ovipositing in McIntosh apples and Bluehaven blueberries during field release experiments.

Species tested	Host plant	
	McIntosh apple	Bluehaven blueberries
R. pomonella	11/41=0.27 (a,d)	10/41=0.24 (b,e)
R. mendax	0/42=0 (a,c,e)	25/42=0.60 (b,c,d)

Values followed by the same letter (a,b,c,d, or e) are significantly different from each other at the P=0.01 level using the G-test of independence.

oviposition in apples by *mendax* females is consistent with electrophoretic data (Berlocher 1980; Berlocher and Bush 1982; Feder et al., unpublished) that found no evidence of *mendax* or *mendax x pomonella* hybrids in adults reared from apples. The low larval-to-adult viability of transplanted *mendax* larvae in apple fruits (14 percent compared to 39 percent in blueberry fruits; Bierbaum and Bush 1988), the results of electrophoretic studies, and data on ovipositional preferences indicate *mendax* females do not utilize apple as a host plant.

Surprisingly, *pomonella* females laid roughly equal numbers of eggs in apples and blueberries under field cage conditions. This was unexpected since prior studies indicated *pomonella* flies did not infest blueberries in nature (Bush 1966; Berlocher 1980; Prokopy and Berlocher 1980; Berlocher and Bush 1982). *R. pomonella* females, however, have laid viable eggs in blueberry

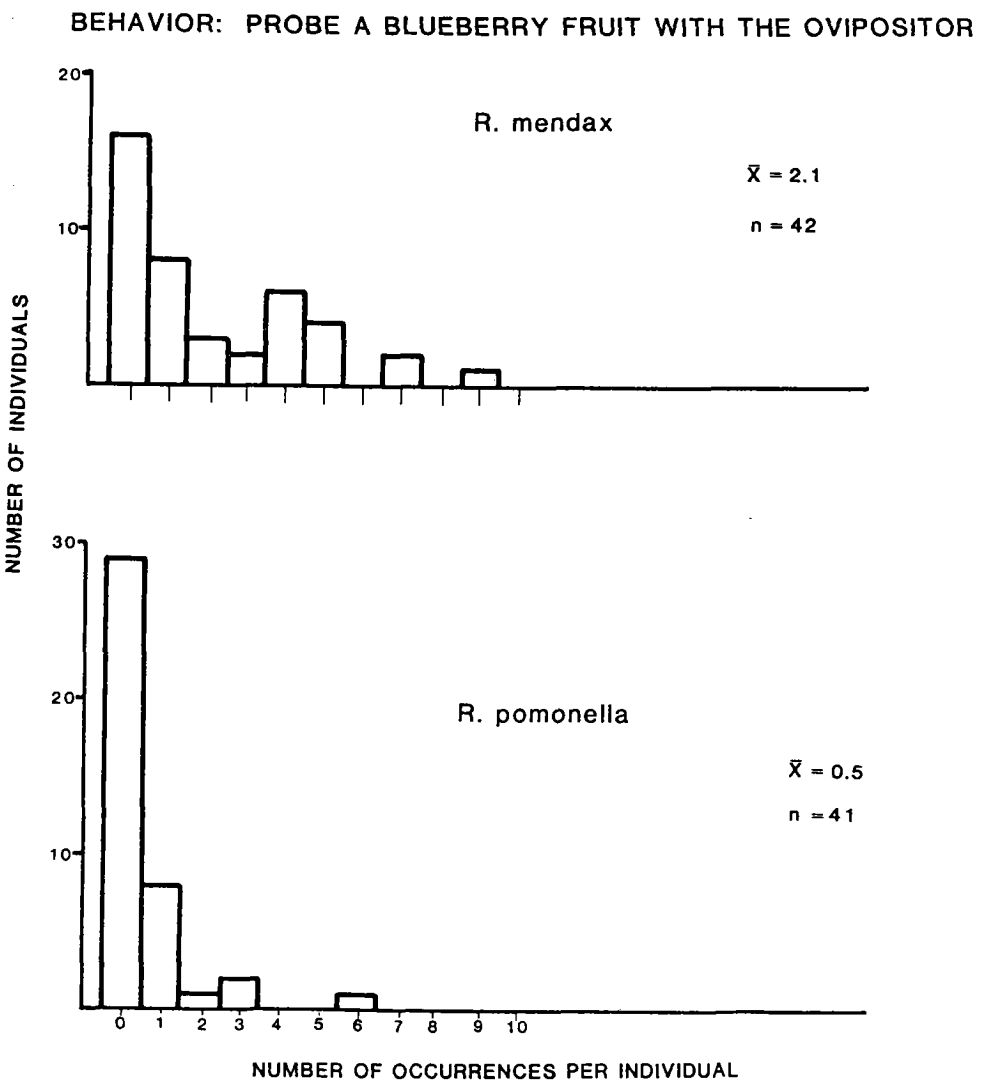

Figure 5B. Number of occurrences of the probing behavior by *R. mendax* and *R. pomonella* females on blueberry fruits.

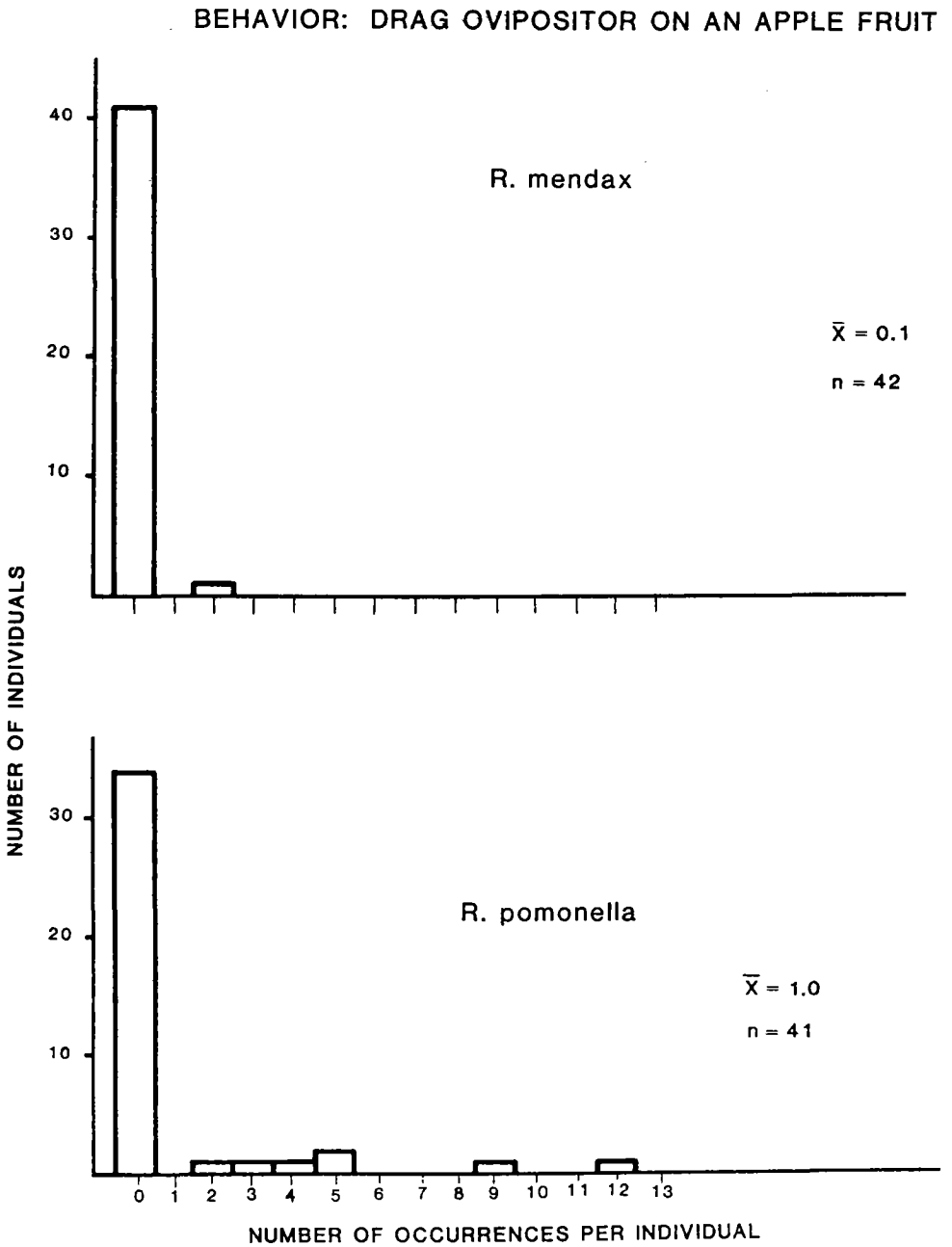

Figure 6A. Number of occurrences of the dragging behavior by *R. mendax* and *R. pomonella* females on apple fruits.

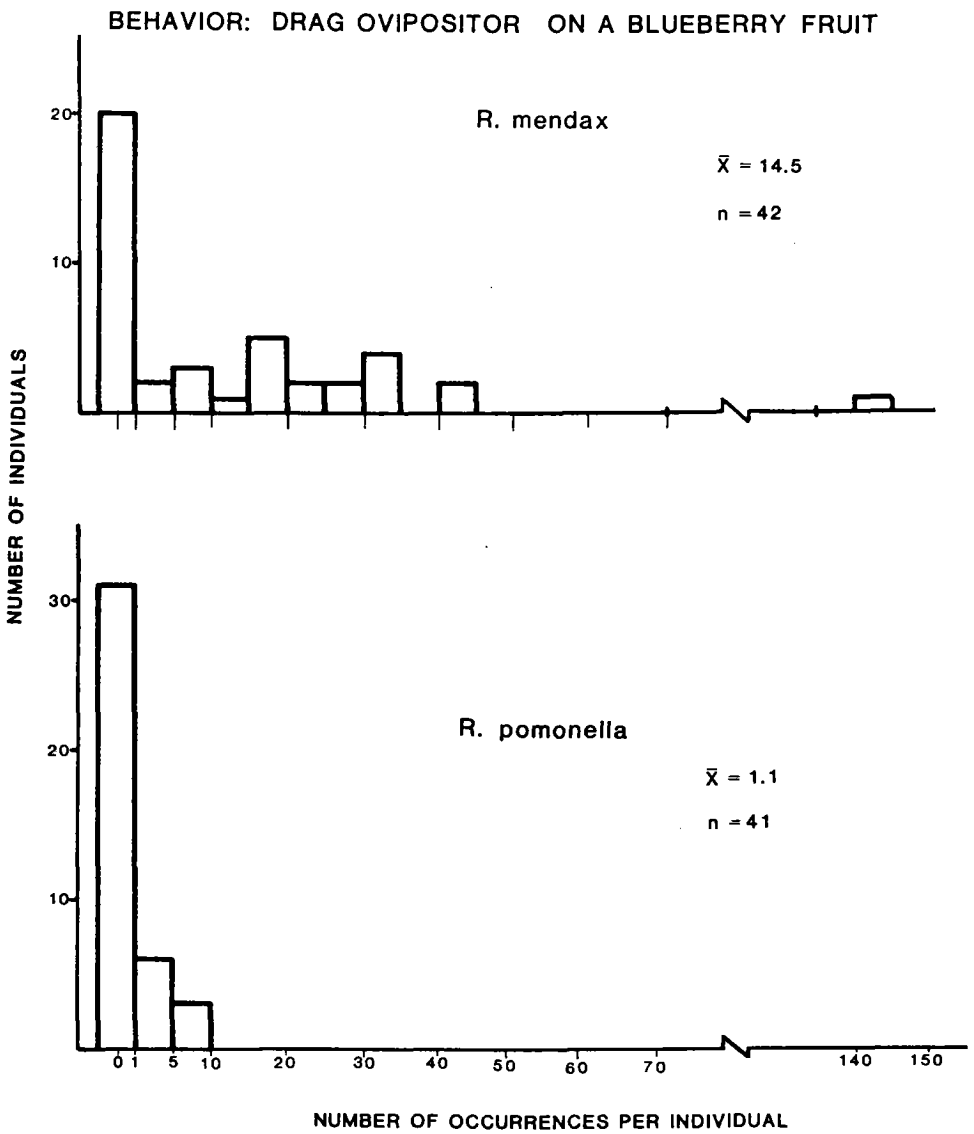

Figure 6B. Number of occurrences of the dragging behavior by *R. mendax* and *R. pomonella* females on blueberry fruits.

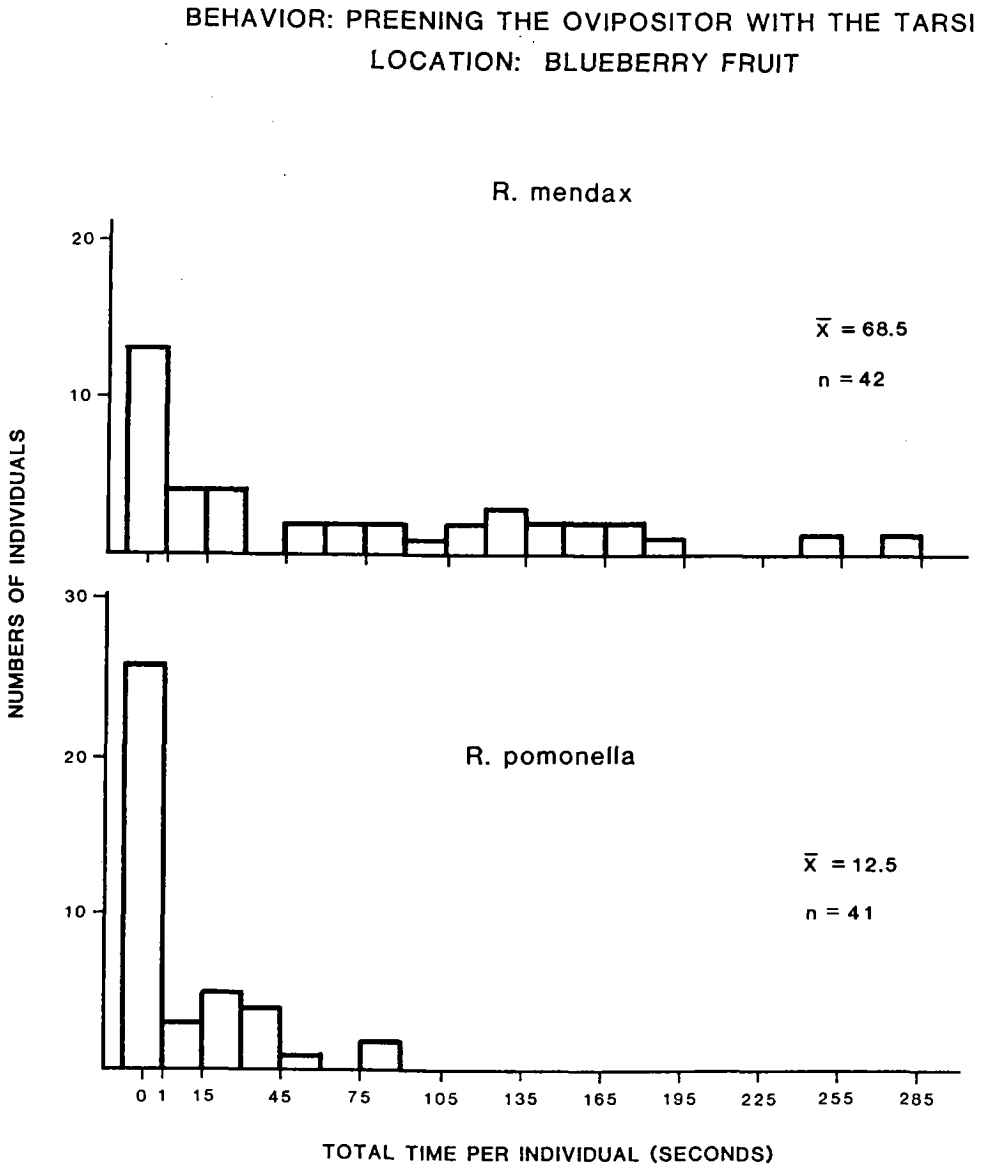

Figure 7A. Total time spent by *R. mendax* and *R. pomonella* females in the ovipositor preening behavior on blueberry fruits.

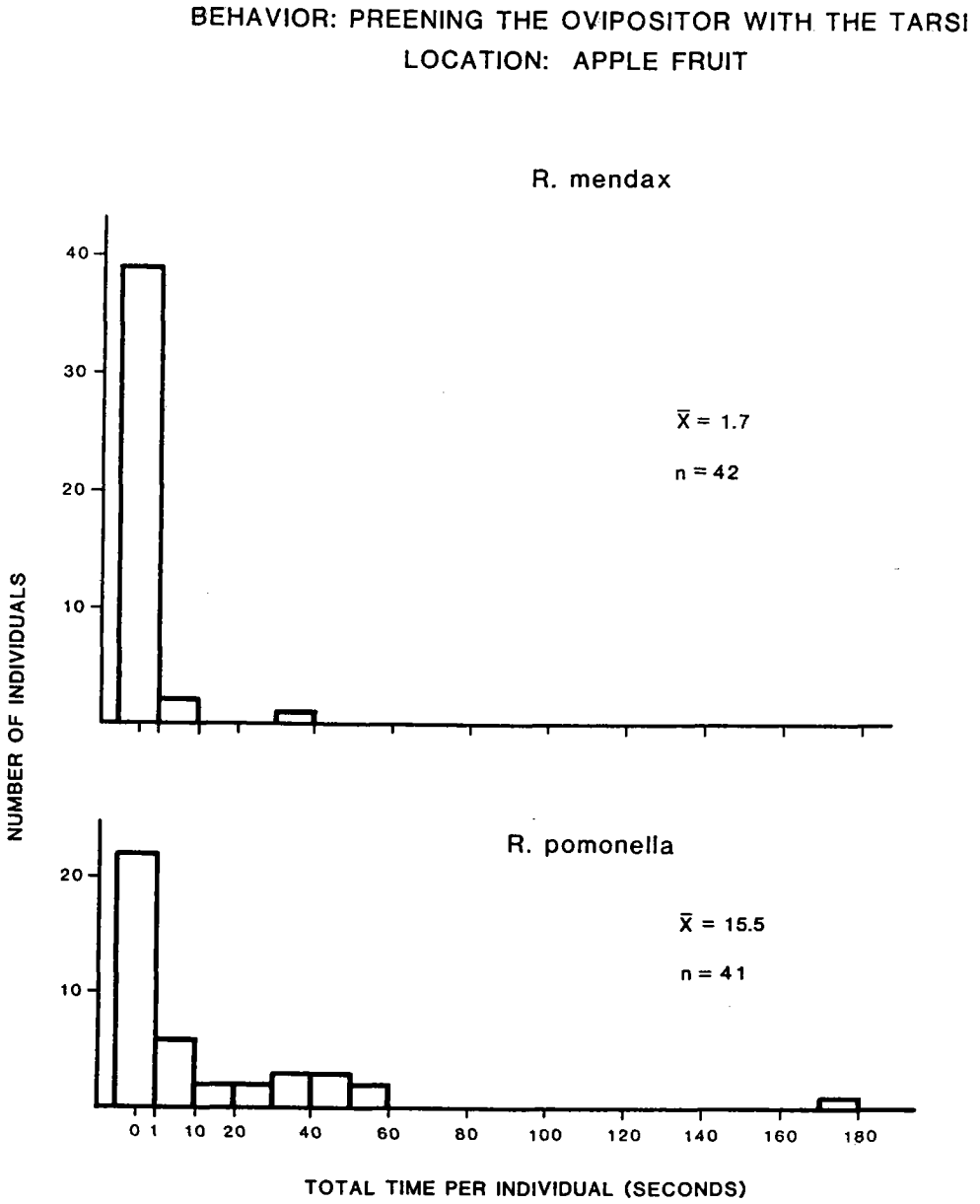

Figure 7B. Total time spent by *R. mendax* and *R. pomonella* females in the ovipositor preening behavior on apple fruits.

fruits when caged for several days on the branches of blueberry plants (Pickett 1937; Pickett and Neary 1940). Diehl and Prokopy (1986 and pers. comm.) are performing host selection experiments on *mendax* and *pomonella* flies that address a subset of topics covered in our own studies. In the laboratory 30 percent of their *pomonella* females oviposited in Red Delicious apples and high bush blueberries, but in field experiments using the same host fruits none of the *pomonella* flies oviposited in blueberries. The reason for this difference between their field and laboratory results is not discussed in their paper, but their field results do not agree with our results and the experiments of Pickett and Neary (1940) that showed *pomonella* females readily oviposited in blueberry fruits under field cage conditions.

Diehl and Prokopy (1986) also asserted that data did not support the designation of *mendax* and *pomonella* as distinct species. This conclusion is not consistent with the empirical evidence, and we do not agree with their assessment. Electrophoretic studies (Berlocher 1980; Berlocher and Bush 1982; Feder et al. unpublished) have determined that the species maintain unique alleles at four enzyme loci in both sympatric and allopatric populations. Consistent morphological differences between the species have been established for ovipositor length, wing band ratios (Bush 1966), male genitalia (Curran 1932; Bush 1966), and pupal dimensions (Bierbaum and Bush, manuscript). Interspecific mating trials and no-choice ovipositional experiments (McAlister and Anderson 1935; Pickett 1937; Pickett and Neary 1940) have indicated that these behavioral traits are involved in the reproductive isolation between the species. No F_1 pupae were obtained from crosses between *mendax* females and *pomonella* males caged on apple and blueberry plants, whereas the reciprocal cross produced F_1 pupae on both fruits. Hybrid adults were also produced from the latter cross, but the larval-to-adult survivorship was lower for hybrids compared to progeny from within species crosses (Bierbaum and Bush 1988). Therefore, the formation of interspecific hybrids in nature is unlikely. If this event occurs, it would most likely result from *pomonella* females mating *mendax* males and ovipositing in blueberry fruits. Thus, any occasional gene flow between the species should be primarily unidirectional from *pomonella* to *mendax*. Additional traits that could serve as mechanisms of reproductive isolation have not been thoroughly studied. These include differences in the prealighting host finding behaviors of *mendax* and *pomonella* males and females and the mating ability, ovipositional behavior, and viability of hybrid progeny.

In addition to differences in their ovipositional behaviors, *mendax* and *pomonella* females showed large differences in: i) residence times on leaves and fruits, and ii) examining and acceptance behaviors tightly linked with oviposition. The examining behaviors included touching the surface of the fruit with the mouthparts (lapping), antennating, and probing the fruit

with the ovipositior; behaviors following oviposition included dragging the ovipositor on the fruit surface and preening it with the hind tarsi.

Compared to *mendax* females, *pomonella* females spent more time on both the fruits and leaves of apple plants, and the reverse relationship held for the mean residence times of the two species on blueberries. A large fraction of the differences in residence times on fruits was due to differences in examining, probing, and dragging behaviors. *R. mendax* flies displayed these behaviors more often than *pomonella* on blueberries, and the reverse pattern was observed on apples. The species investing the most eggs in a fruit also completed more ovipositor draggings on the fruit surface. This is consistent with prior experimental evidence indicating that the dragging behavior is tightly associated with oviposition into a fruit (Prokopy 1972).

The lapping, antennating, and probing behaviors probably provide essential chemosensory information, stimulating a female to oviposit into or depart from the fruit. Recent studies that have characterized chemosensilla on the ovipositor, tarsi, and antennae of *pomonella* flies have identified two longitudinal groves at the apical portion of the ovipositor contain chemosensilla that respond to NaCl solutions (Liscia et al. 1982). Contact chemosensory sensilla have been identified on the tarsi of *pomonella* females by Bowdan (1984), who found that different cells within a sensillum showed distinct electrophysiological responses to ovipositional-deterrent pheromone, sucrose, and salt solutions. Fein et al. (1982) used apple volatiles to study electroantennogram responses of *pomonella* males and females, and found a variety of GLC-fractioned apple extracts stimulated antennal sensilla. With the exception of the study by Fein et al. (1982), few experiments have tested the responses of *mendax* or *pomonella* chemosensilla to naturally occurring fruit compounds, and there is a need for more electrophysiological work with such compounds.

A few studies by other researchers have tested for evolutionary divergences in the adult host acceptance behaviors of closely related populations and species of insects infesting different host plants. One experiment established clear differences in the preferences of sympatric host races. In an interesting set of greenhouse experiments, Phillips and Barnes (1975) observed differences in ovipositional preferences of races of codling moths infesting apples, walnuts, and plums. They found the apple race strongly preferred apple plants, and the walnut and plum races preferred walnut trees over both apples and plums. The ovipositional preferences of walnut x apple and plum x apple F_1 hybrids were intermediate to the wild parental populations, indicating a genetic basis for differences in preference.

A high degree of specificity in ovipositional preference has

also been established for host races of sawflies infesting balsam fir, black spruce, and white spruce (Knerer and Atwood 1972; 1973), and closely related species of gall-forming tephritid flies (Huettel and Bush 1972). In both studies, laboratory choice experiments revealed a virtually complete ovipositional preference for the host plant infested by each race or species in nature. Huettel and Bush (1972) studied the genetic basis of host selection using F_1, F_2 and backcross hybrids, and found that genetic variation at a single locus could explain the differences in preference between the species.

Several other studies have found allopatric populations within a species that have diverged in host preferences or larval viabilities in response to variation in the abundance of alternate plants in different geographic regions (e.g., Singer 1971, 1983; Hsiao 1978; Carson and Ohta 1981; Rausher 1982; Tabashnik 1983; Papaj 1986). In several of these examples, evolutionary changes in host preference have occurred during a host range expansion in which one or more locally abundant host plants were added to the total number used by the species. Although these studies have helped clarify the nature of evolutionary differentiation between populations of phytophagous insects, an improved understanding of the phenotypic and genetic bases of behaviors controlling differential host plant use by closely related insect species is essential. By continuing our analysis of host examining and acceptance behaviors of *mendax, pomonella*, and their hybrid progeny, we hope to understand the genetic bases of these behavioral traits. The methods we have developed permit detailed step-by-step analyses of differences in key host acceptance behaviors displayed by each species on blueberry and apple plants. Through focusing on the inheritance of these traits, we hope to gain an improved understanding of characters thought to be important in the formation of host races and species of *Rhagoletis* fruit flies. We believe this approach can also provide insights into behavioral mechanisms controlling colonization of plants by insect herbivores.

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SUMMARY

Our study focuses on the host examining and acceptance behaviors of two sibling species of *Rhagoletis* fruit flies infesting different rosaceous and ericaceous host plants. Field cage experiments tested for differences in the post-alighting behaviors of mated *R. mendax* and *R. pomonella* females on apple and blueberry plants. These experiments utilized a portable microcomputer to provide a quantitative, sequential record of the host examining and acceptance behaviors displayed on both host plants and pinpointed differences between the species in key post-alighting behaviors. This quantitative behavioral approach determined significant behavioral differences amenable to further genetic analysis, and provided essential information for understanding the evolutionary processes involved in host race and species formation.

There were several differences in the examining and acceptance behaviors of the species on apple and blueberry fruits. These included: i) touching surface of the fruit with the labellum of the mouthparts (lapping), ii) touching the fruit surface with the tip of the third antennal segment (antennating), iii) bending the abdomen and probing the fruit with the ovipositor for egg laying, iv) dragging the ovipositor on the fruit to deposit an oviposition-deterring pheromone, and v) preening the ovipositor with the tarsi. The differences between the species in their preovipositional behaviors were correlated with differences in the percentage of females laying at least one egg in a fruit. The percentage of *mendax* females ovipositing in Bluehaven blueberries was significantly higher than the percentage of *pomonella* females; the opposite pattern was observed on the fruits of McIntosh apple plants. In addition, the numbers of eggs laid per *mendax* female in blueberries was higher than the number of eggs per *pomonella* female, and the reverse pattern was found in apple fruits. *R. pomonella* females resided for longer periods of time on apple fruits and leaves than *mendax* flies, and the reverse relationship held for the time spent by each species on blueberry fruits.

Our continuing analysis of host examining and acceptance behaviors displayed by *R. mendax, R. pomonella,* and their hybrid progeny should help ascertain the phenotypic and genetic bases of behaviors controlling differences in the host plant use of these closely related species. By focusing on these behaviors, we hope to gain an increased understanding of characters thought to be important in the formation of host races and species of *Rhagoletis* fruit flies.

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CHAPTER 5

Management of the Apple Maggot in the Eastern United States

W. H. Reissig

Status and Importance of the Apple Maggot as a Fruit Pest:

The apple maggot, *Rhagoletis pomonella*, is still considered to be the key insect pest influencing total insecticide usage in apple orchards in the northeastern United States and Canada because more insecticide is used annually for apple maggot control than against any other single insect pest in apple orchards. However, the apple maggot is a relatively easy insect to control with conventional insecticides and, consequently, significant or detectable apple maggot fruit infestation in commercial orchards in the northeast is quite rare. Most apple orchards in the northeastern United States are in relatively close proximity to wooded or semi-wooded areas with numerous hosts for the apple maggot, either unsprayed or wild apple trees or hawthorn. Therefore, orchards may be continually be threatened by flies immigrating into the orchards from outside sources.

Control Tactics:

At present, the use of chemical insecticides is the only viable apple maggot control tactic that is suitable for large-scale use in commercial orchards throughout the northeast.

Principles of Apple Maggot Control with Insecticides:

It is generally assumed that commercial apple orchards have either very low or no indigenous populations of apple maggot because of the demonstrated effectiveness of insecticides against the flies and the low levels of damage observed in treated orchards. Therefore, control sprays are targeted against flies immigrating into orchards from unsprayed outside habitats. The objective of protective insecticide programs is to kill gravid females moving into sprayed trees before they can oviposit.

Selection and Usage of Insecticides:

The organophosphate insecticides, azinphosmethyl and phosmet, are currently the most widely used materials to control apple maggot in the northeast. Figure 1 (Reissig et al. 1983) illustrates the effectiveness of azinphosmethyl in killing gravid apple maggot females continuously exposed in the laboratory to

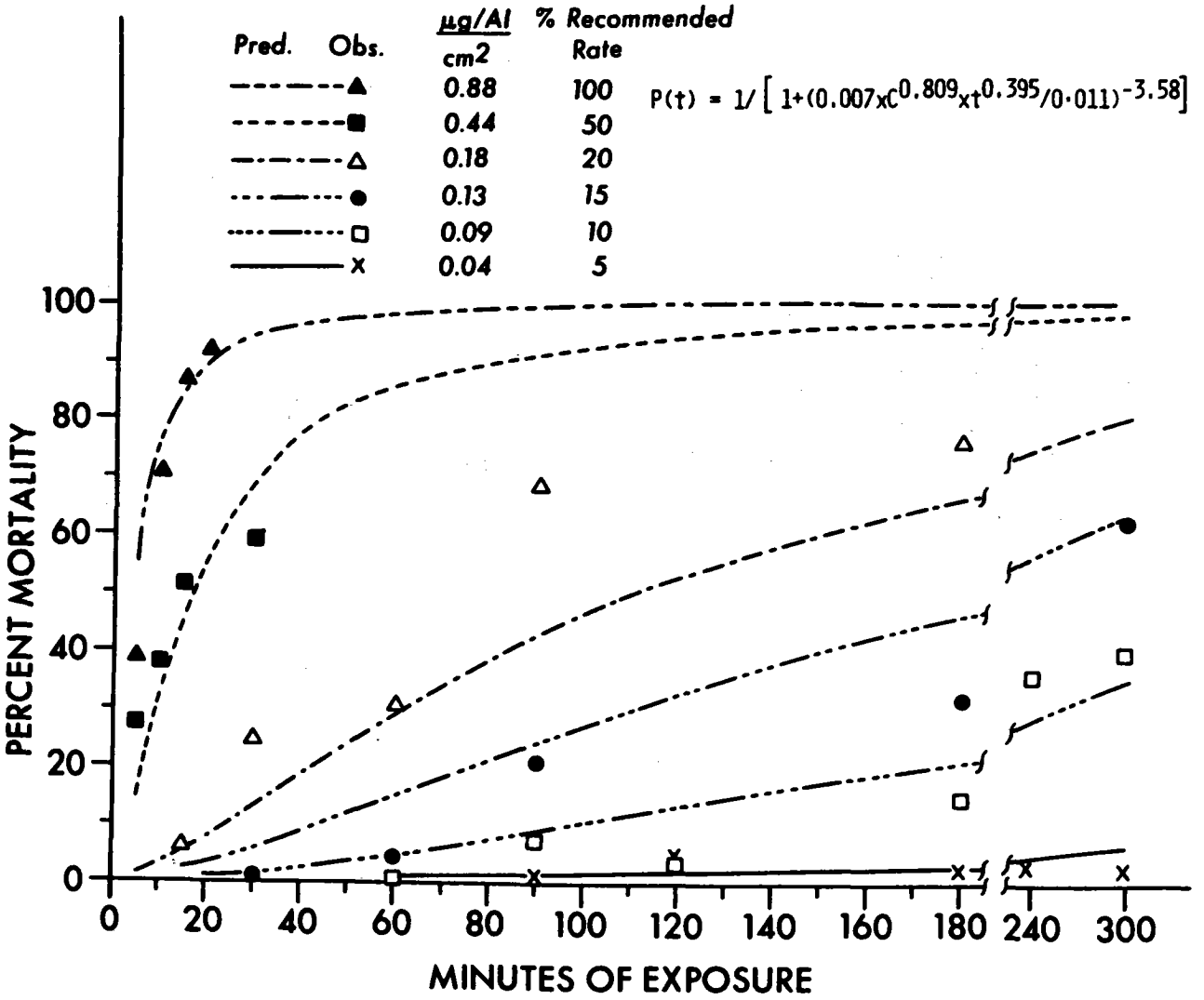

Figure 1. Comparison of observed and predicted mortality from continuous exposure of apple maggot females to different rates of surface residues of azinphosmethyl for various time periods.

surface residues of the material. At the field rate, 39 percent mortality occurred after only five minutes of exposure, and 92 percent mortality occurred after 20 minutes. However, in laboratory bio-assays using fruit and gravid females, the females oviposited in 5 percent of the apples treated with the recommended rate of azinphos-methyl even though all were killed in 48 hours of exposure. This laboratory data agrees with field observations that slight amounts of apple maggot damage can occur in orchards surrounded by sources of flies, apparently because a few females migrating into the trees can oviposit before they are killed.

Scheduling of Insecticide Treatments in Commercial Apple Orchards:

Despite all of the research work done on apple maggot monitoring systems, which will be discussed later in this presentation, the great majority of commercial apple orchards in the northeast are not monitored for the apple maggot, and spray treatments are still applied on a protective basis. The traditional grower timing schedule for apple maggot sprays with respect to fly abundance is presented in Figure 2. This four-spray schedule requires an initial spray about seven days after the first observed apple maggot fly emergence (first part of July), then subsequent sprays near mid-July, first part of August, and near mid-August.

Personnel in the Cornell tree fruit IPM program have recommended that growers delay the first apple maggot spray until (a) the flies have emerged generally throughout a region which is indicated by regular trap catches at a number of different monitoring sites in unsprayed areas; and (b) apple maggot flies have been regularly trapped on perimeter traps in commercial orchards, indicating that flies have begun to immigrate into commercial orchards from unsprayed habitats. Such a strategy based on apple maggot trap catches in both unsprayed habitats and commercial orchards has resulted in the type of modified spray schedule illustrated in Figure 3. Due to the delay in initial application, growers influenced by the IPM program are applying an average of only about three sprays annually for apple maggot control instead of the former four sprays. Table 1 illustrates this type of scheduling by summarizing the estimated average numbers of sprays applied for apple maggot control on farms owned by several typical growers monitored by our Cornell fruit IPM program from 1977 to 1985. The actual numbers of treatments have remained relatively constant during this period and have averaged around three sprays annually. It is very difficult to analyze growers' spray records in orchards in the northeast and determine how many sprays are actually applied to control apple maggot because many other insect pests, such as leafrollers, San Jose Scale, codling moth, leafminers (*Phyllonorycter* spp.), aphids, and white apple leafhoppers, are also active in commercial apple

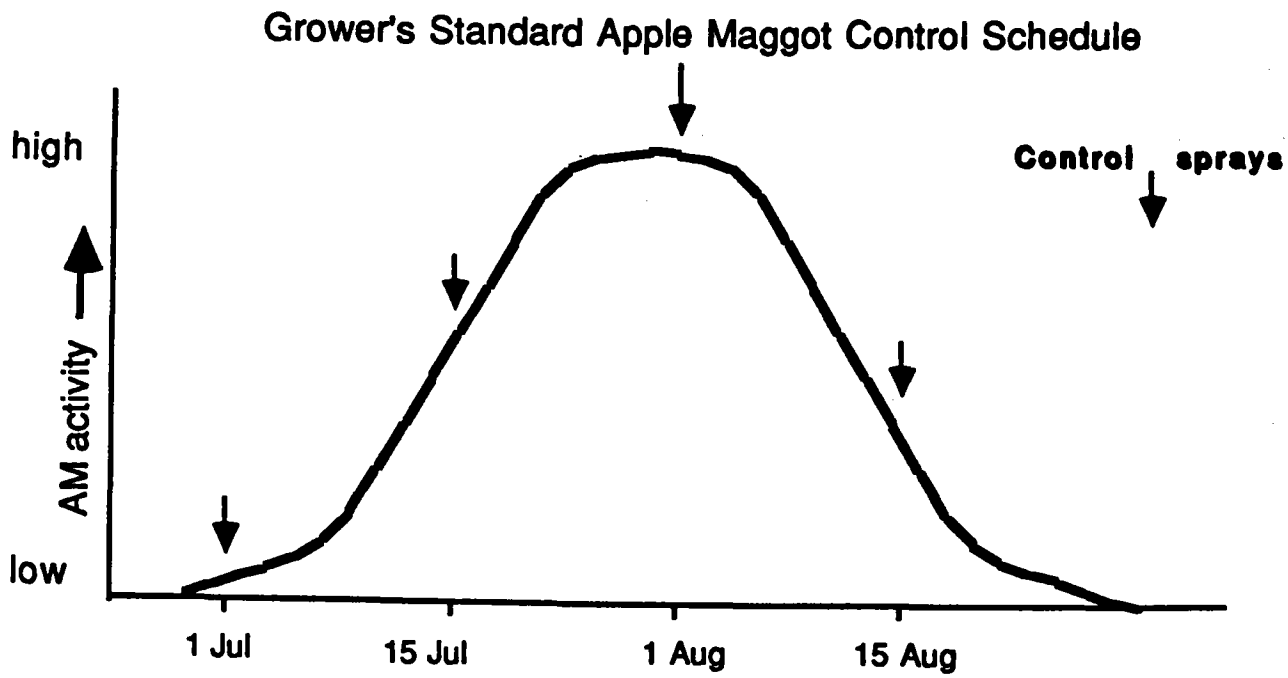

Figure 2. A hypothetical schedule of a New York apple grower's standard protective control schedule for control of the apple maggot.

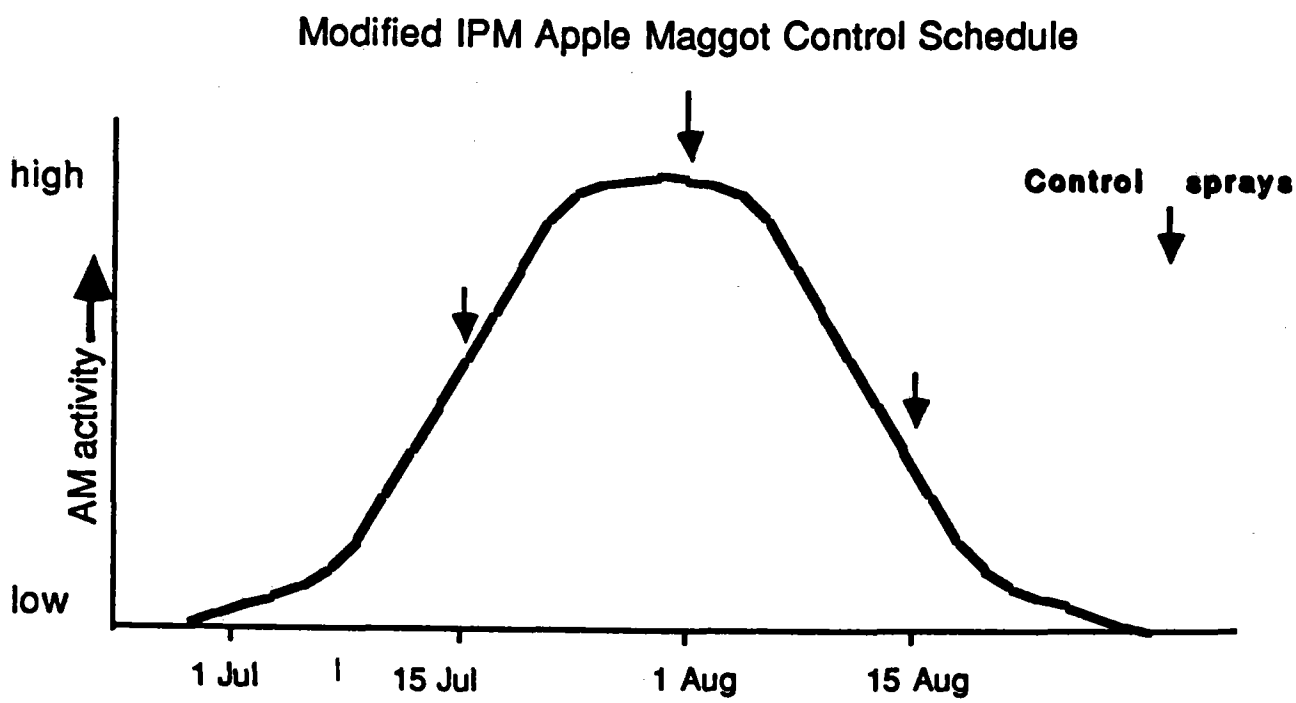

Figure 3. A hypothetical schedule of a New York apple grower's modified apple maggot control schedule based on recommendations from the tree fruit IPM program.

Table 1. Number of July and August sprays using an insecticide effective against the apple maggot (Wayne Co., N.Y.).

	$\bar{x}$ Number of Sprays Per Year		
Grower	1976	1979	1984
Vermeulen	2.6	3.0	3.9
Wagemaker	2.8	2.3	4.0
Verdow	3.0	4.0	2.7
Henry	2.7	3.8	2.7
Average	2.8	3.4	3.3

orchards during July and August. Obviously, broad spectrum sprays applied against any of these other pests will also provide protection against the apple maggot. In a practical sense, this diversity of insect pests in orchards in the northeast during late summer is a key factor limiting a grower's acceptance of alternate apple maggot management strategies. The growers assume that even if they do not have to spray to control apple maggot, they will still have to apply control treatments against the rest of the pest complex and, consequently, their overall usage of insecticides will remain the same.

Biological Relevance for Terminating Apple Maggot Sprays in Mid-August:

As previously discussed, growers in New York and many other apple-growing areas of the northeast traditionally do not apply any insecticide after mid-August. Figure 4, which summarizes the seasonal catches of apple maggot on traps along the edges of 20-25 commercial apple orchards in western New York, indicates that substantial numbers of flies are immigrating into orchards in late August and September. Despite this late-season fly activity occurring in the absence of protective spray residue in September, no significant amounts of apple maggot damage are observed at harvest, even though flies are active and the un-protected, nearly mature fruit should be suitable for ovi-position. This is a phenomenon which should be investigated more closely in the future to determine the implications for apple maggot management during late summer.

Potential Tactics for Improving Insecticide Efficiency Against the Apple Maggot

Monitoring Systems:

Because most commercial apple orchards in the northeast apparently do not have large indigenous apple maggot populations, it should theoretically be possible to improve the efficiency of insecticidal control by monitoring populations in individual orchards so that sprays are applied only when necessary instead of on a protective basis in every orchard when adults are active throughout a region. I would like to summarize the results of cooperative efforts by research and IPM personnel in New York State in testing apple maggot monitoring systems in commercial orchards during the last 10 years.

The relative efficiency of several different monitoring systems that have been tested in New York orchards from 1977 to 1985 is shown in Table 2. Assuming that the populations of flies remain somewhat constant in these same representative orchards from year to year, the catches presented here reflect the relative efficiency of the Pherocon apple maggot yellow panel, unbaited red sticky spheres, and spheres baited with a synthetic

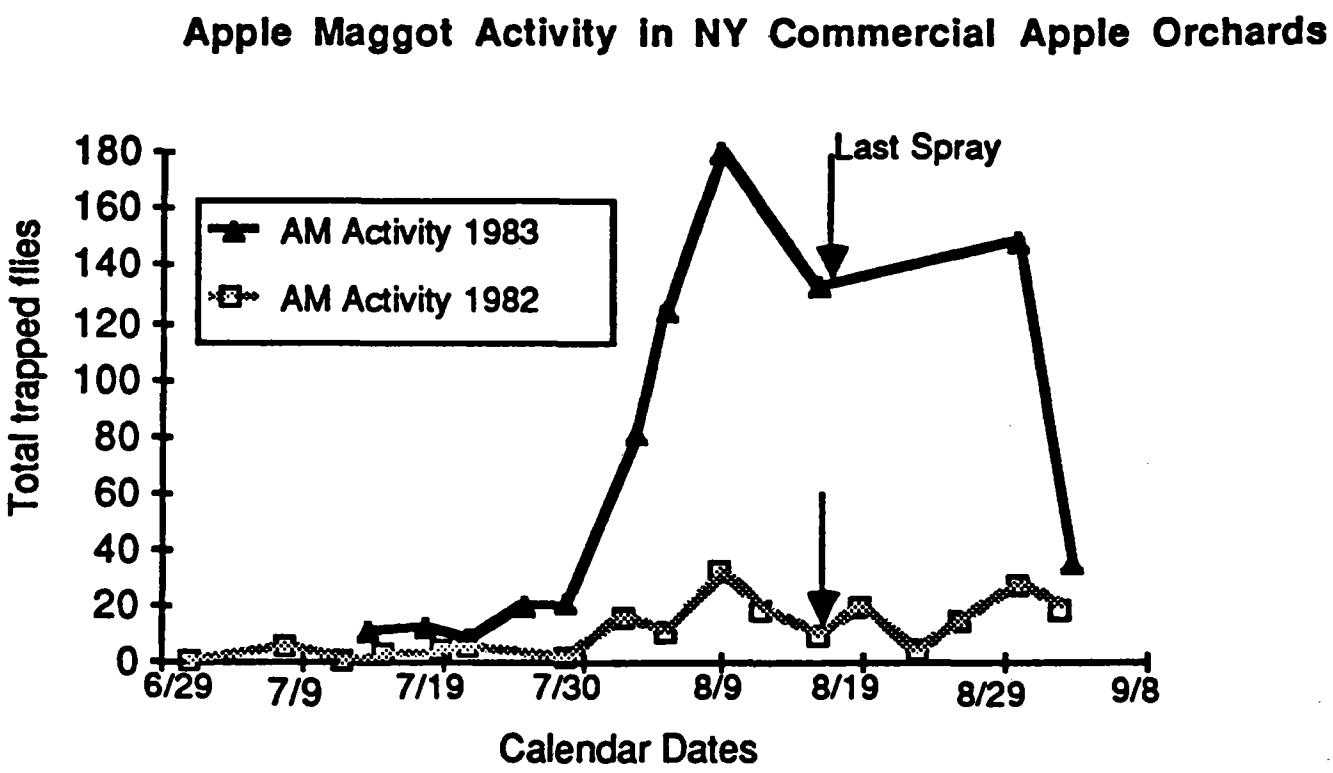

Figure 4. A comparison of seasonal activity of apple maggot in New York commercial orchards as indicated by catches on perimeter monitoring traps.

Table 2. Comparison of apple maggot fly catches on three different types of traps (Senco Farms, Wayne Co., N.Y.)

	$\bar{x}$ AM Catch/Trap/Year		
	1977	1985	
Farm	Pherocon AM Yellow Panel	Unbaited Red Sticky Sphere	Volatile Baited Red Sticky Sphere
Weed	1.33	1.5	23.0
Vandeusen	1.6	3.6	21.2
Todd	1.5	4.7	22.6
Kelley	0	3.5	14.75
Average	1.24	3.16	20.75

apple volatile apple maggot attractant mixture in capturing flies in New York commercial orchards. Our perceptions of the abundance of apple maggot flies immigrating into commercial orchards in New York have changed a great deal as different monitoring systems have been used.

When orchards were monitored with Pherocon panels during late 1970's, usually only a few flies were captured in all of our monitored orchards, and frequently no flies were captured at a given trap site throughout the season. Therefore, we assumed that apple maggot immigration was low in most commercial orchards, and some orchards had absolutely no detectable flies. After the program switched to red spheres in the early 1980's, following some embarrassing incidents in which infested fruit was detected in commercial orchards which had not been sprayed because no flies were captured on Pherocon panels monitoring the blocks, catches per trap in the same orchards went up and there were very few sites at which no flies were captured. Catches on the volatile-baited spheres have been much higher during the last several years of tests in the commercial orchards and some apple maggot flies have been captured on almost every volatile-baited trap, even when no catches had been reported in the orchards using other monitoring systems. Therefore, our most recent conclusions about apple maggot populations in commercial orchards in western New York State derived from tests of monitoring systems are as follows:

1. Virtually every orchard has at least a few flies immigrating in from outside sources every year.
2. Many orchards have substantial numbers of flies immigrating into the perimeter of the block.
3. Since damage in these orchards is usually insignificant, even when unsprayed check plots are left along the border, oviposition from normal populations of flies immigrating into orchards is usually not sufficient to cause detectable damage even in orchards with reduced spray schedules.
4. Probably, the trace amounts of oviposition resulting from these small populations of immigrating females are too low to allow the establishment of indigenous populations of flies in the orchards.

Recent Tests of Volatile-baited Monitoring Systems:

Whenever apple maggot monitoring systems using Pherocon panels or standard red spheres have been used to monitor individual commercial orchards in New York State, a spray is recommended whenever one fly is captured. Then, subsequent catches are ignored for 10-14 days because the spray residue is assumed to provide protection against any flies entering the orchard during this interval. After this interval, the procedure starts again. Obviously, whenever we tested this system with volatile-baited spheres, catches were so high that sprays were

applied in almost every monitored orchard every 14 days. Therefore, during the last several years, we have been testing the volatile-baited spheres in commercial orchards using higher catch spray action thresholds.

Table 3 summarizes the results from a test conducted in 1983, in which four treatments were compared in 10 commercial orchards in Wayne county, New York.

1. IPM Modified Protective Program - A protective spray every 10-14 days starting in mid-July and ending near mid-August.
2. Monitoring with unbaited spheres - A spray was applied whenever one apple maggot per trap was captured.
3. Monitoring with volatile-baited spheres - A spray was applied using a threshold of a total capture of two flies on three volatile-baited spheres per orchard.
4. Monitoring with volatile-baited spheres - A spray was applied using a threshold of a total capture of four flies on three volatile-baited spheres per orchard.

Since there were no significant differences in the numbers of control sprays or damage among the four programs, future tests were set up to test the volatile-baited spheres using higher thresholds.

Conceptual Limitations of Apple Maggot Monitoring Programs:

Several oversimplified or unrealistic assumptions are used in our current apple maggot monitoring programs. For example, insecticide residues following a spray are assumed to be completely effective in killing adults and preventing oviposition during an arbitrary time period (10-14 days), and then become completely ineffective. Also, only crude assumptions are made via the trapping thresholds about the populations of flies immigrating into the orchards and their potential for subsequent damage.

HESGAM System:

The HESGAM computer model, Harvest Evaluation Simulator for the Effects of Guthion on Apple Maggot Damage, which was developed at Geneva, New York, represents an attempt to deal more realistically with the some of the key variables influencing apple maggot management in a commercial apple orchard.

The overall logic of the model is shown in Figure 5. Inputs required by the model are spray and rainfall history, apple maggot catch to date (using volatile-baited spheres), the estimated orchard yield, size of a fruit sample being evaluated for apple maggot damage, and the acceptable risk of detecting apple maggot damage. The model then goes through several intermediate steps to calculate the predicted oviposition to date, and

Table 3. Tests of different spray action thresholds for volatile-baited spheres (Wayne Co., N.Y., 1983).

Program	Avg. flies/ 3 traps	Avg. No. Sprays	%Infested Fruit Avg.	Range
Standard Program	———	2.6	0.1	0-1.3
Unbaited Spheres	———	2.0	0.1	0-0.6
VBS[1/] 2 Fly Threshold	69.2	2.7	0.1	0-0.4
VBS[1/] 4 Fly Threshold	78.3	2.3	0.7	0-6.3

[1/] Volatile-baited spheres.

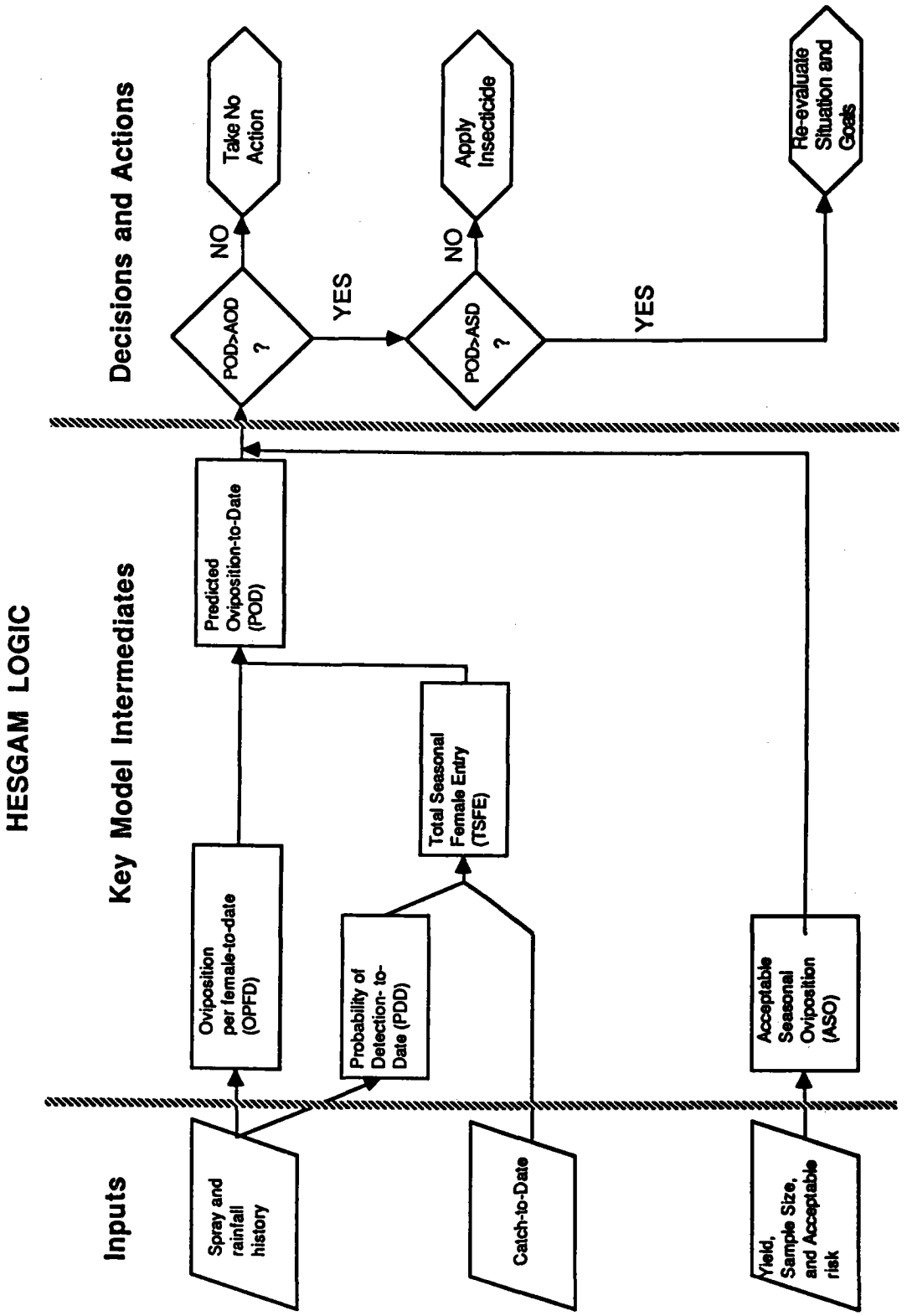

Figure 5. Flow chart of logic used in the HESGAM model.

the acceptable oviposition to date. Based on these calculations the grower will be advised to either take no action or to apply an insecticide.

The model was actually tested in the field in small sections of nine commercial orchards in western New York State during 1985. Table 4 summarizes the results in the tested blocks. An average of 1.6 apple maggot control sprays was applied in the test blocks and observed damage in the test blocks was negligible. Although these initial results appear to be encouraging, it should be mentioned that the number of sprays and damage observed in subplots treated by the model were quite similar to those observed in adjacent plots in the same orchards in which conventional apple maggot monitoring systems of volatile-baited spheres (three apple maggots per trap threshold), and unbaited spheres (one apple maggot per trap threshold) were used.

The basic problem with the accuracy of the model is shown in Figure 6. It tends to predict more apple maggot damage than is actually observed as indicated by the relatively large number of observations of zero damage in orchards in which substantial amounts of damage were predicted by the model.

In closing, I would like to say that our future research in apple maggot management will probably continue to focus on three general areas: (a) improvement of volatile-baited monitoring systems, (b) improvement of the HESGAM management model, and (c) development of simplified insecticide application schedules based on fruit oviposition suitability, seasonal apple maggot immigration patterns into commercial orchards, and apple maggot behavior and ecology during late August and September.

Table 4. Field tests of the HESGAM model for AM management (Wayne Co., N.Y., 1985).

Block	Total Flies	#Flies/ Trap	# Sprays	%Damaged Fruit
29	35	17.5	1	0.0
9	7	3.5	0	0.1
23	35	11.6	2	0.0
280	52	13.0	1	0.7
245	87	29.0	2	0.8
465	123	61.5	3	0.0
155	92	46.0	3	0.7
84	38	19.0	2	0.4
101	62	20.6	1	0.1
Average	59	24.6	1.6	0.3

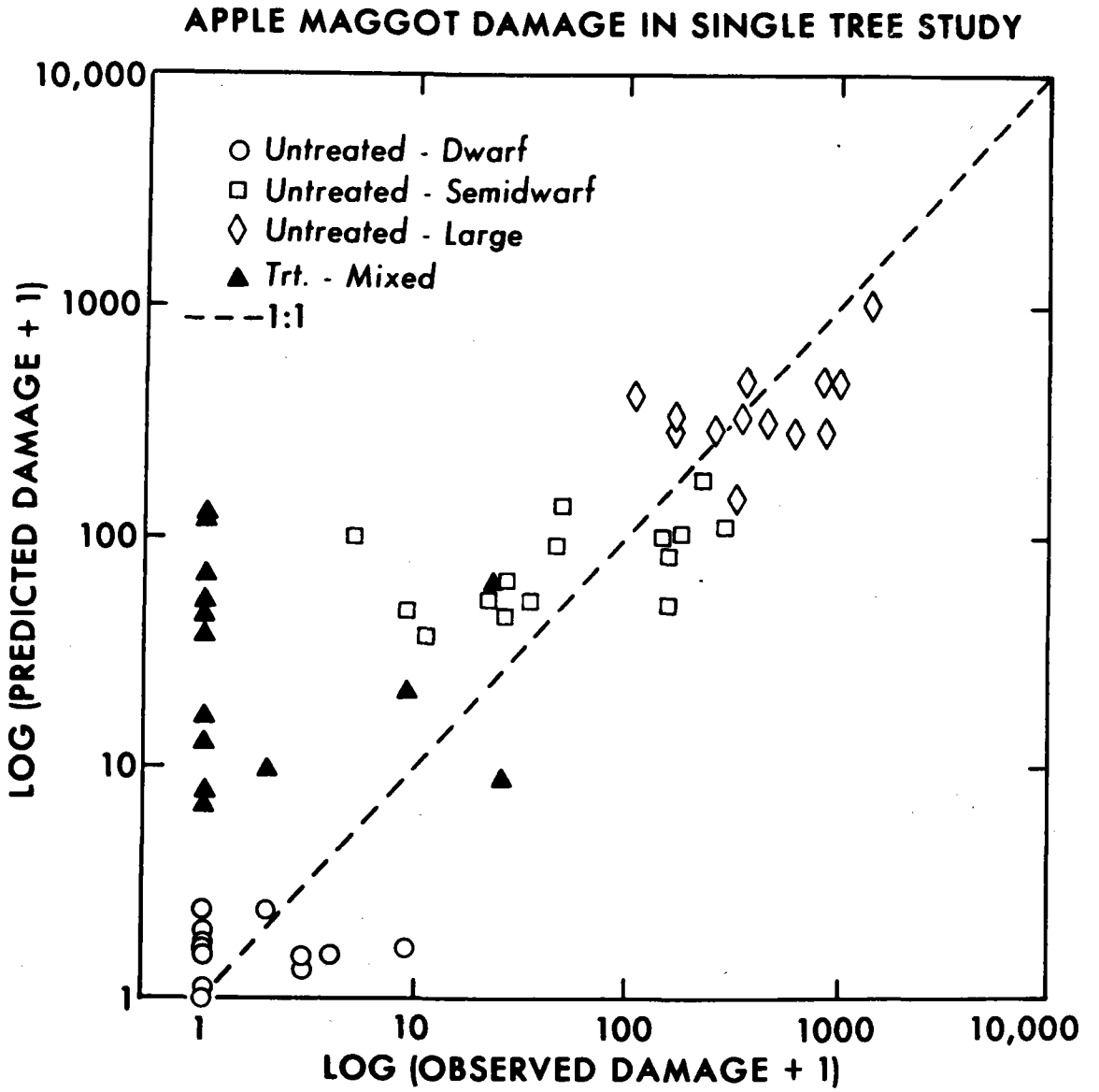

Figure 6. A comparison of observed versus predicted apple maggot damage in a single-tree study.

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CHAPTER 6

Apple Maggot Management in the Western United States

M. T. AliNiazee

The apple maggot, *Rhagoletis pomonella* (Walsh), is now established in at least six western states, including Oregon, Washington, California, Idaho, Utah, and Colorado (AliNiazee and Brunner 1986). In western Oregon and southwestern Washington, the pest density is high enough to cause concern. The apple growers of the Willamette Valley, Oregon, have reluctantly accepted the presence of another important pest and are planning to cope with it by use of insecticides. Fortunately, the apple maggot is an easy insect to control. Most of the registered insecticides provide effective suppression of the pest.

Other major apple-producing areas of the Pacific Northwest, including Hood River Valley, Oregon, and eastern Washington, have embarked on a pest-exclusion program which is based on large-scale monitoring for any incoming flies using Pherocon^{R} AM traps. They will attempt to eradicate the pest as soon as it is found by employing a 3-5 year program of host removal from about a 1/2-mile zone immediately surrounding the area where a fly was found, and by spraying infested areas with Imidan at frequent intervals. A quarantine program was also approved in Washington during 1984, which restricts the inter- and intra-state movement of fruit from infested areas. The quarantine prohibits the entry of all host fruit from eastern United States and non-commercial backyard fruit into and within the state from Utah, Idaho, Oregon, and California. Commercial apples are regarded as potential hosts if an apple maggot is found within 1/4-mile of a commercial apple orchard. Similar quarantine programs are also in effect in Oregon and California.

Pest Distribution Surveys

Active survey programs are currently underway in practically all states of the Pacific Northwest. The survey programs of Oregon and Washington are aimed at delimiting the distribution of apple maggots and to provide better support base for making decisions regarding the application of pest control tactics. The Oregon program, which was started nearly eight years ago, has been instrumental in developing an understanding of the pest in the western United States. A detailed distribution of this pest in Oregon was reported by AliNiazee and Westcott (1986) and in Washington by Brunner (1987). In general, apple maggots are well distributed throughout the Willamette Valley of Oregon, with

isolated infestations along the coast, southern Oregon, and the Hood River Valley. Continuous distribution is also found in southwestern Washington and isolated finds were reported from Spokane and a few other areas of Washington. The only commercial apple-growing area infested by apple maggots in the western United States occurs near Salem, Oregon. Otherwise, most of the apple maggot finds in the western United States were associated with abandoned and uncared for apple trees and hawthorn, both native (*Crataegus douglasii*) and introduced ornamental (*C. monogyna*) species. Isolated infestations of prunes in the Willamette Valley (AliNiazee 1985) and cherries in Utah (Jorgensen *et al.* 1986) have also been noticed.

The distribution of the apple maggot in the Pacific Northwest is probably directly related to the distribution of its host plants. Where the host continuum occurred, the natural distribution of the pest was noticed. However, this spread was limited to a few yards or at the most a few miles (Maxwell and Parsons 1968, Neilson 1971). It appears therefore, that most of the major distribution probably occurred through movement of infested host material. As a matter of fact, a more careful analysis of five-year distribution data in Oregon (AliNiazee and Westcott 1986) does suggest that most of the early disjunct distribution probably occurred by transport of infested fruit. This mode of distribution is probably responsible for most of the apple maggot distribution throughout the west.

Trap Evaluation and Monitoring in Commercial Orchards

Most of the information available on trap effectiveness comes from the studies conducted in the eastern United States and Canada (Kring 1970, Neilson *et al.* 1981, Reissig 1975, 1982, and Prokopy and Hauschild 1979). In addition to trap types, it appears that trap placement is also an important contributing factor to trap efficacy (Drummond *et al.* 1984). Reissig (1975) determined that red sphere traps were effective in commercial orchards while relatively little difference was found between the Pherocon AM and red sphere traps in abandoned orchards. Reissig *et al.* (1985) reported that addition of an apple volatile extract (consisting of a mixture of hexyl acetate, butyl 2-methyl butyrate, propyl hexanoate, hexyl propionate, butyl hexanoate, and hexyl butanoate in a 36:7:12:5:29:11 ratio) improved the performance of the red spheres as an apple maggot trap. AliNiazee *et al.* (1987) reported that a Ladd trap consisting of an unbaited yellow panel, with a red sphere in the center and an apple volatile attractant, was among the most effective traps for apple maggot monitoring. This trap was effective both under low and high population density situations. MacCollom (1986) used this trap in a trap-out study and obtained highly encouraging results. Although the price of this trap is very high at present, thus making it uneconomical for general use, further reduction in cost and increased usage will undoubtedly bring the

price down and make it possible to use it in large-scale programs. It appears that for the survey and the trap-out control purposes, this might be an ideal trap because of its increased effectiveness over what is presently available.

Management Choices

The management of apple maggots in Oregon and Washington falls in the categories of local eradication, containment, quarantine, and seasonal control using summer sprays. The local eradication is currently pursued in two major fruit-growing areas of the Pacific Northwest. At the Hood River Valley, a local eradication program has been pursued for the past five years. As soon as a fly is found in a given trap, a half-mile area surrounding that particular find is sprayed on a regular basis using Imidan. The area is intensely trapped, number of traps increased, and counts are taken more frequently. In addition, a large number of fruit will be cut open and examined for maggot infestations. A similar program has also been pursued in a local eradication program at Spokane, Washington (Brunner 1987).

Area-wide eradication appears difficult because of the abundance of available host material and lack of precise information regarding pest distribution. Moreover, the cost of such a program could be excessively high and may not justify its consideration as a viable option.

Both Oregon and Washington have pursued a containment approach during the past five years. The approach involves insecticide-treated and host-removed buffer zones around commercial orchards where flies have been caught. A host removal program has been applied extensively in Washington state in an attempt to limit fly distribution on its own.

The containment and local eradication programs are successful only if the quarantine restrictions are strictly enforced and general awareness and cooperation of the public is obtained. As mentioned before, most of the new infestation and introduction are probably man-made by movement of infested fruit.

The localized eradication may delay the outcome and restrict establishment for many years. However, the flies will eventually get established in these areas. The containment and suppression of a new infestation in a new area by extensive use of insecticides is also limited in scope, but it, nevertheless, provides a delaying response to the onset of apple maggots. When this is applied in all marginal areas, it may help reduce the infested zones, thus lowering the general level of populations and potential new infestations.

AliNiazee (1986) reported the inadequacy of relying on codling moth, *Cydia pomonella* L. cover sprays to control apple

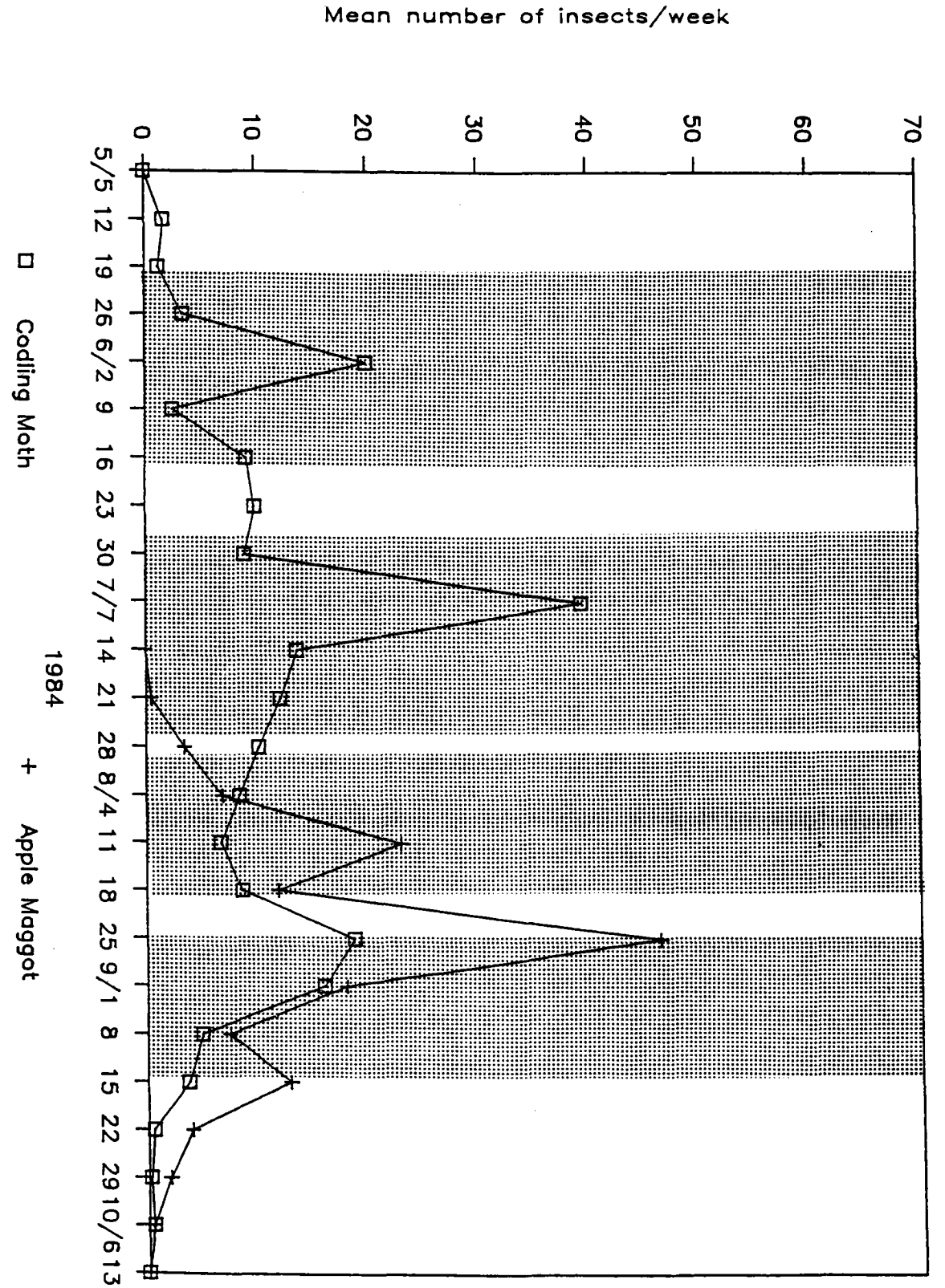

Figure 1. Adult emergence curves for codling moth and apple maggots-1984. The unshaded areas indicate times of vulnerability for apple maggot attacks in commercial orchards.

maggots in most commercial orchards. Further studies conducted during 1984-86 substantiated earlier results. For instance, the first codling moths emerged in 1984 on May 8 in the Willamette Valley. The first apple maggots were not noticed until July 18. But once the apple maggots emerged, the fly populations peaked at a time when very little, if any, codling moth spraying was going on in the orchards. There were repeated time intervals throughout the late summer and early fall when the apple maggots were capable of getting into apples. These "windows of vulnerability" (the unshaded areas in Figure 1) make it almost impossible to depend solely on codling moth sprays for control of apple maggots. A similar situation was noticed in 1985 season (Figure 2). It is also interesting to note that none of the commercial orchards of Oregon and Washington have any breeding populations of the apple maggot. Thus the problem arises outside the orchards, and the flies move to the commercial orchards late in the season in search of suitable oviposition sites. Consequently, late-season varieties are especially affected by the apple maggot.

Extensive monitoring of commercial orchards in the Willamette Valley (Figure 3) during 1985 suggests that most of the fly movement to commercial orchards occurred in September (AliNiazee and Westcott 1987). Thus late summer and early fall sprays become essential. In some orchards more than one spray might be needed. Most of the commercial growers of the Willamette Valley, where the apple maggots are generally prevalent, pursue a program of using indicator traps and applying insecticides as soon as the flies are detected in their orchards. It appears that all the registered compounds, including azinphosmethyl, phosmet, phosalone, and diazinon, provide adequate fly control. During past years we tested ultra-low-volume (ULV) sprays of malathion for the control of apple maggots. Preliminary data indicate that this technique is adequate in controlling apple maggots. Further tests with ULV malathion and bait sprays are currently underway at our laboratory.

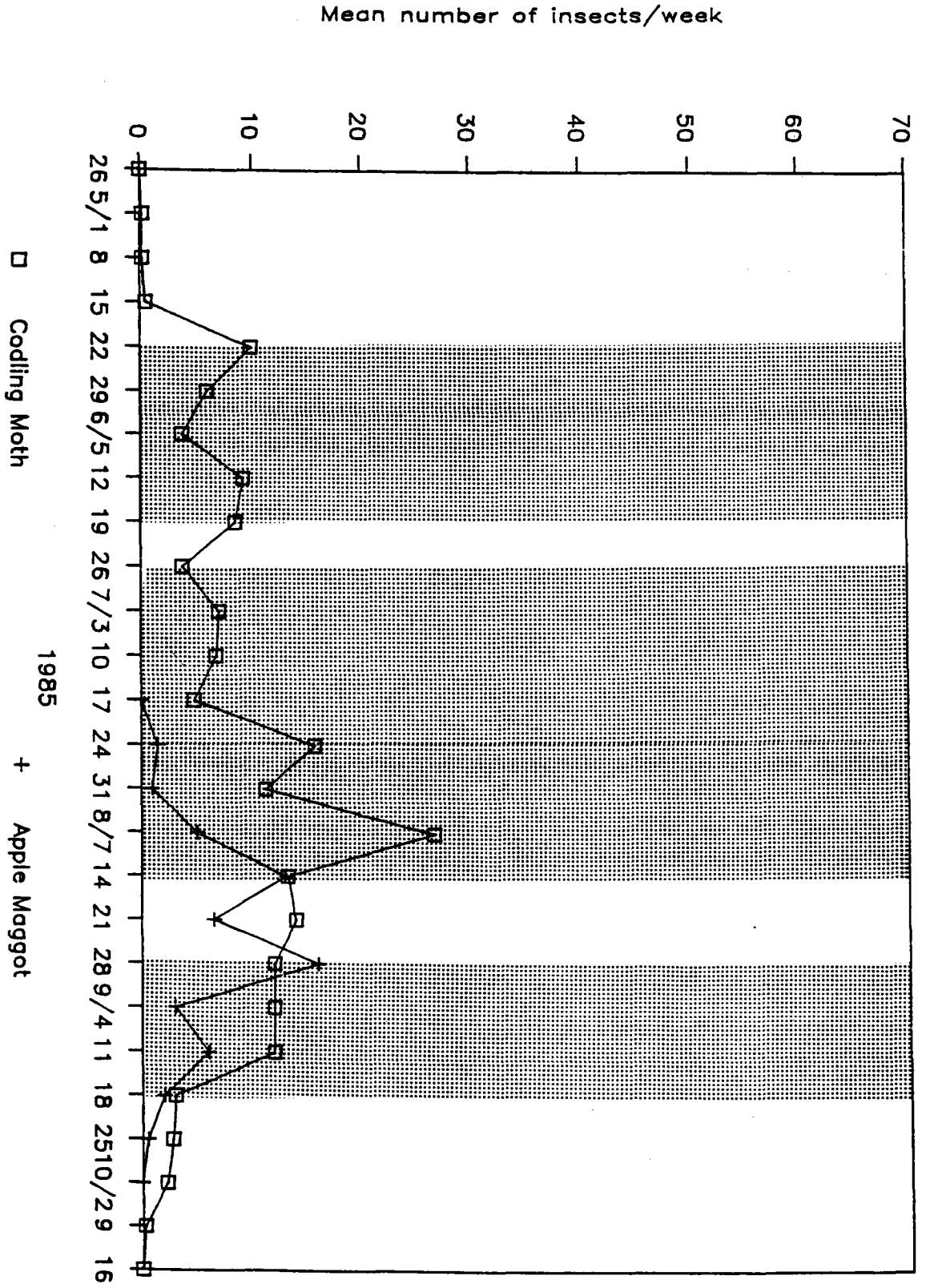

Figure 2. Adult emergence curves for codling moth and apple maggots-1985. The unshaded areas indicate times of vulnerability for apple maggot attacks in commercial orchards.

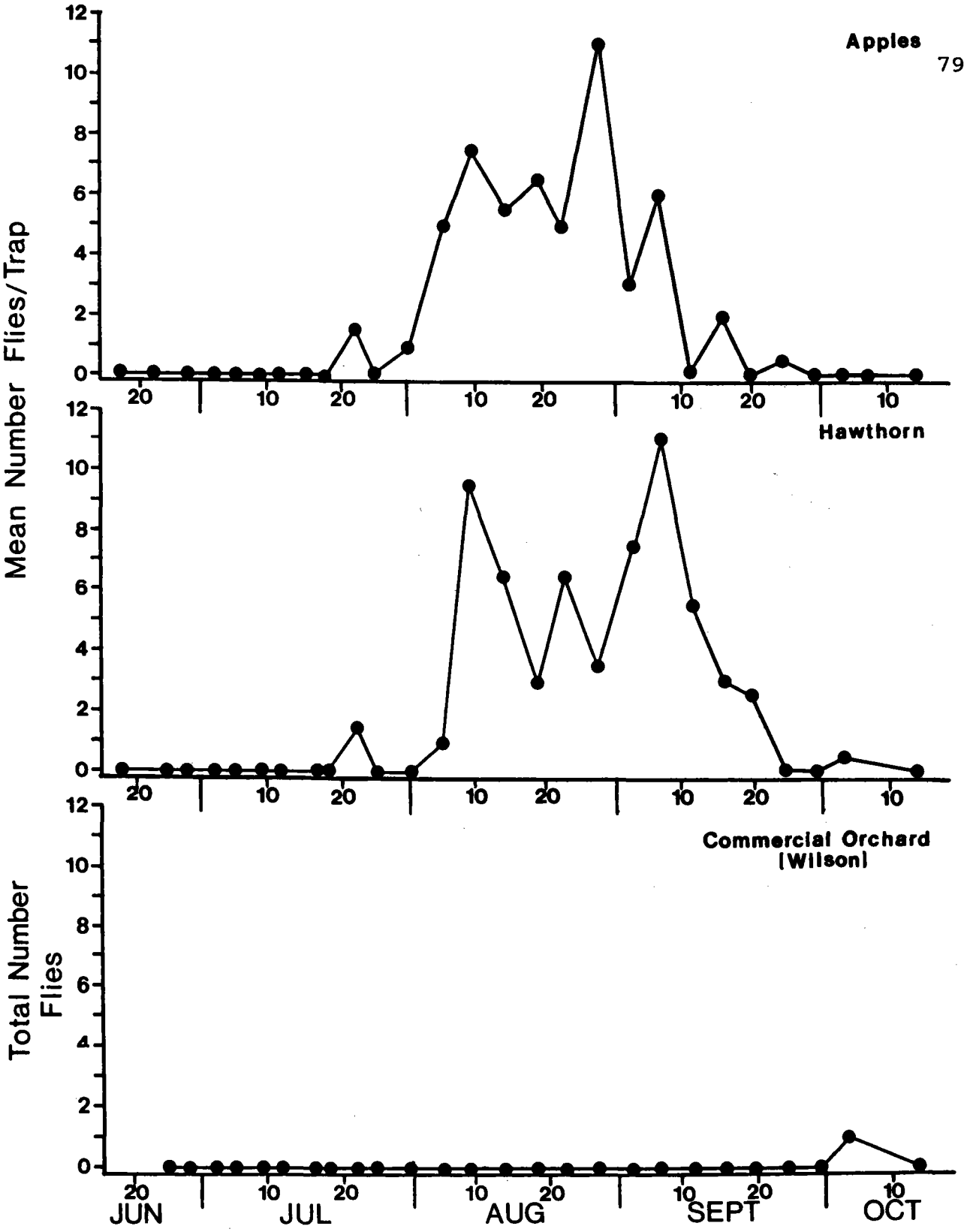

Figure 3. Apple maggot trapping pattern in three different habitats; an abandoned apple tree patch, a hawthorn patch, and a commercial apple orchard-1984.

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CHAPTER 7

Detection, Quarantine, and Eradication of Fruit Flies Invading Florida

Richard A. Clark and Howard V. Weems, Jr.

The Florida Department of Agriculture and Consumer Services, Division of Plant Industry, and the United States Department of Agriculture have maintained fruit fly traps throughout the state since the 1956 Mediterranean fruit fly eradication campaign. Probably no program in which the Division or Plant Industry is engaged is more important or stands to benefit Florida agriculture more than fruit fly detection.

The purpose of this report is to provide the reader with the history and evolution of fruit fly detection and eradication techniques utilized in Florida over the past 56 years.

The 1929 Mediterranean Fruit Fly Eradication Campaign

The value of Florida's Fruit Fly Detection Program can be well justified when the history of some of the past fruit fly eradication programs is considered. The first infestation of an economic fruit fly in Florida occurred on April 6, 1929, when a state nursery inspector became alarmed because of the presence of "maggots" in grapefruit which he acquired in the vicinity of Orlando, Florida. Examination of these larvae by E. W. Berger, entomologist, and G. B. Merrill, Associate Entomologist, led them to conclude that a fruit fly of the family Tephritidae was involved, possibly *Anastrepha fraterculus* (Wiedemann), which, at that time, was believed to occur in the West Indies and was commonly referred to as the West Indian fruit fly. This conclusion was also shared by D. B. Mackie, Senior Entomologist of the California Department of Agriculture, who happened to be in Florida, and by C. T. Green, Dipterist of the Bureau of Entomology in Washington. On April 9, 1929, Authur C. Brown, accompanied by several Plant Board inspectors, arrived in Orlando and promptly got in touch with W. W. Yothers, in charge of the Bureau of Entomology laboratory in that city. Shortly after his arrival, a man appeared at the laboratory and reported an excessive drop of grapefruit had taken place at the G. L. Hamlin 40-acre citrus grove located at Marks and Mills Streets, Orlando. A visit to that citrus grove followed, and an examination of the fallen fruit revealed the presence of many fruit fly larvae. Upon further observation, adults were to be seen resting on and flying among the foliage. Some were captured and mailed to Washington and Gainesville by W. W. Yothers and Arthur C. Brown, respectively. These were identified on April 10, 1929, as the

Mediterranean fruit fly, *Ceratitis capitata* (Wiedmann) (State Plant Board Campaigns: Eradication of the Mediterranean Fruit Fly 1929, 1958).

The Chief of the Plant Quarantine and control Administration, C. L. Marlott, and the Plant Commissioner of the State Plant Board, Wilmon Newell, approached the problem with one objective - eradication, although this had never been accomplished in any country in which the Mediterranean fruit fly had become established. A plan of approach was agreed upon and, as might be expected, modifications were made from time to time. Essentially the program embraced the following features:

1. Scouting to determine the extent of its spread in Florida and elsewhere.
2. Division of the state into (a) Infested Zones, to include any property within one mile of an infested grove or area in which infested host fruits or vegetables were located; and (b) Protective Zones, to include an area within nine miles of the outside boundary of an infested zone.
3. Destruction of all host fruits and vegetables in infested properties as rapidly as found, including the destruction of such material in the surrounding mile (infested) zones.
4. Application of poisoned bait spray throughout both infested and protective zones. The first formula employed consisted of lead arsenate, 8 lb; crude brown sugar, 50 lb; molasses, 10 gal; water, 100 gal. (Almost 300,000 lb of lead arsenate were used). Later (October 1929) the lead arsenate was reduced from 8 to 4 lb, and finally the lead arsenate was replaced by copper carbonate and the formula changed to read: Copper carbonate, 8 lb; syrup (black strap molasses), 5 gal; sugar (soft brown), 25 lb; water, 100 gal. Complaints were received concerning spay injury, which resulted in the appointment of a committee of successful citrus growers to investigate the claims. To summarize, the committee reported in part "that the beneficial results of the 'bait spray' far outweigh the damage that has occurred." (Author 1931, p. 55-56.)
5. Establishment of a summer host-free period by removing and destroying all summer-ripening host fruits and the prohibition of the growing of summer-ripening vegetables in both infested and protective zones.
6. Removal of all citrus and other host fruits or vegetables (throughout the year) in the infested zones prior to their reaching a stage of ripeness making them susceptible to fruit fly attack, including the prohibition of planting such vegetables in the infested zones "until the State Plant Board, with the approval of the United States Department of Agriculture, shall determine that all infestations in such zone have been eliminated and that the restrictions of this paragraph shall no longer remain in force with respect thereto."

7. Requirements of orchard and packing house controls, control of transportation in interastate commerce, control of motor vehicle and other road movement and other features of sanitation and protection enforced under state authority within the infested and protective zones.

The eradication area embraced approximately 10 million acres of land which included a total of 120,000 acres of citrus and about 160,000 acres devoted to noncitrus; 1,002 infested properties were involved, distributed over 20 counties (Alachua, Brevard, Citrus, Duval, Flagler, Hernando, Hillsborough, Lake, Levy, Marion, Osceola, Pasco, Pinellas, Orange, Polk, Putnam, St. Johns, Seminole, Sumter, Volusia) extending from the Atlantic Ocean to the Gulf of Mexico; 72 percent of the bearing citrus trees which in 1929 produced 73 percent of the crop; much of the remaining area was unimproved land including areas of swamp, hammock, cut-over pine lands, cypress forest, and marshes (State Plant Board Campaigns. Eradication of the Mediterranean Fruit Fly, 1929, 1958).

McPhail traps played an important part in the eradication program, serving in a triple capacity: (a) in infested properties they served as an index to the adult population; (b) in what were believed to be noninfested areas, they assisted in detection of adult flies not discoverable by any other means; and (c) they made it possible to determine the effectiveness of control measures and, in a few instances, the first record in a given area resulted from catching adults in the traps. At one period as many as 12,645 traps were scattered throughout the affected areas.

A single trap caught in one day as high as 81 adult flies, and 1,644 flies were caught by this means prior to August 1929. The lure used in the McPhail trap was kerosene, which was found to be attractive to the male fruit flies.

The eradication of the Mediterranean fruit fly in Florida after the build-up of a tremendous population in 1,002 infested properties ranks as one of the outstanding entomological miracles of the age. The Mediterranean fruit fly was finally declared eradicated in late 1930, at a cost of $7,573,136.91.

The 1956 Mediterranean Fruit Fly Eradication Campaign

The second invasion of an economic species of fruit fly became evident on April 13, 1956, when Mr. O. L. Prior, 93 N.W. 93rd Street, Miami Shores, Florida, found insect larvae in grapefruit that he was preparing to eat. He called the Miami Herald and they referred him to the Assistant County Agent, Douglas M. Knapp. Mr. Knapp carried the larvae to Dr. D. O. Wolfenbarger, Entomologist, at the Sub-Tropical Experiment Station, Homestead. Dr. Wolfenbarger recognized the possibility of these larvae being Mediterranean fruit fly (*Ceratitis capitata*

(Wiedmann)). He contacted Mr. C. E. Shepard, regional inspector for the State Plant Board. One larva was forwarded to the entomological department at Gainesville, and two larvae were forwarded to Dr. W. L. Popham, Director of the Crops Regulatory Program, Agricultural Research Service, Washington, D.C. The single larva received in the Gainesville office on April 18, 1956, was identified by State Plant Board Entomologist, Dr. Howard V. Weems. Jr., as the Mediterranean fruit fly.

On April 18, 1956, Mr. Ed L. Ayers, the Plant Commissioner, directed Mr. H. A. Denmark, Acting Chief Entomologist, to go to the infested area in Miami to collect adults with McPhail traps.

On April 19, 1956, Mr. Denmark met C. E. Shepard and E. F. Miles and traps were placed on the properties of Messrs. Prior, 93 N.W. 93rd Street; Dario Mazzoleni, 71 N.W. 93rd Street; and A. Scheeschmidt, 101 N.W. 93rd Street. Eleven adults of the Mediterranean fruit fly were collected in the McPhail traps on the property of Mr. Prior at 8:30 p.m. Mr. Shepard was notified, and a night letter was sent to Dr. Popham as follows: "CAUGHT MEDITERRANEAN FRUIT FLY IN SWEET BAIT TRAPS. AM FORWARDING SPECIMENS."

On April 20, 1956, nine more adults were caught on Mr. Prior's property. Three adults were caught on Mr. Scheeschmidt's property, and one adult on Mr. Mazzoleni's property.

A visit was made to the Sub-Tropical Experiment Station to inform Dr. Wolfenbarger that the infestation was definitely Mediterranean fruit fly. The information was released to the public on April 23 by Mr. Jack Matthews from Lakeland (Denmark 1956).

The methods used in fighting the Mediterranean fruit fly in the 1956 campaign were entirely different than those techniques employed in the first campaign, when host trees and plants were stripped of fruit and produce in order to eliminate breeding spots. This latest campaign involved the most recent technologies, although many of the newest chemicals, such as oil of Angelica seed, were still in the testing stage and were put to use before final laboratory examinations were completed. The old system of fruit stripping and a host-free period was discarded at the outset. Substituted was a new theory of regulation through fumigation and certification, with practically no loss to farmers and growers of produce and fruit.

In general, when a fly infestation was found, a quarantine zone of one mile was established and all host fruit or produce moving out of this quarantine zone had to be fumigated or processed immediately. Weekly spraying for a minimum of 40 days was prescribed for a radius of half a mile around the infestation. Barring further fly finds, the entire area was released

from quarantine restrictions 90 days after recovery of the last fly, or 120 days after the last larval find.

Baited traps were greatly increased within the spray area to serve as guides in determining cut-off dates for controls. Traps also were increased along the outside margin of the spray area to ascertain if flies had escaped to develop a new infestation.

State and federal program officials lost little time in getting the eradication operation airborne. Multi- and single-engine aircraft were called into the struggle to do the spraying which previously had been confined to the ground. By the use of aircraft, the mass application of insecticides was possible over heavily populated areas, often within minutes after an infestation was discovered. Planes could transfer necessary equipment from one area to another with little loss of time.

At the peak of the 1956 medfly program, there were 27 planes in daily operation, ranging in size from B-17's of World War II to single-engine piper cubs. In considering that these planes operated at heights ranging from 50-100 feet above tree tops, the low accident rate was remarkable. In the only fatal mishap, a twin-engine C-84 crashed at Boca Raton on a ferrying trip, killing 2 crew members and 3 helpers who prepared the spray mixture (Cowperthwaite 1956-58). A newly perfected bait spray, which was applied to vegetation by airplanes and ground sprayers, was one of the principal weapons used in the fight against the adult fly. The mixture used in aerial spraying consisted of two pounds of 25 percent wettable malathion, one pound of an approved protein hydrolysate, and enough water to compose one gallon of liquid. Two pounds of Staley Sauce Bait No. 2 were used in the early formulas, with a later switch to Sauce Bait No. 7. This mixture was distributed at the rate of one gallon per acre. The bait spray was applied at intervals of approximately one week, with the length of time between sprayings depending upon the frequency and intensity of rain and upon other climatic conditions (Ayers 1954-56).

Ground and hand equipment were used in the treatment of soil with dieldrin, an insecticide which obtained a high percentage of kill on larvae entering the soil, and a reasonable kill of adult flies emerging from the pupal state. The recommended treatment was 50 pounds per acre of 10 percent granular dieldrin 30-40 mesh.

As an indication of the size and scope of the program in Florida, a total of 800,423 acres was treated with insecticides one or more times. In view of the fact that some areas were covered as many as a dozen times, insecticides were applied to an aggregate total of 6,804,383 acres.

A federal quarantine regulated the movement from Florida to

other states of all articles that might harbor the insect. State regulations controlled movement of these articles to non-infested areas of the state. Regulated articles consisted principally of the following: fruits, vegetables, and other garden and orchard products; sand, soil, earth, peat, compost, and manure; fruit-picking equipment; trucks, wagons, cars, aircraft, boats, and other means of conveyance, and containers used in conveying fruits or vegetables; other products and articles associated with the production of, or commerce in, fruits and vegetables, or that had been or were contaminated with sand, soil, earth, peat, compost, or manure.

At the height of the Mediterranean fruit fly campaign, roadblock inspection stations were operated on highways leading out of heavily infested areas to prevent the spread of the pest through the movement of host fruit and soil. A total of 4,672,901 vehicles were inspected. In spite of the roadblocks, the spread of the medfly followed the main highways leading from the infested areas. This indicated that infested fruit was being carried through the roadblocks or adult flies were trapped inside of vehicles and escaped beyond the roadblocks, therefore all roadblocks were discontinued on October 23, 1956. Program officials approved a total of 264 fumigations chambers in which approximately 5,040,000 boxes of citrus were fumigated with ethylene dibromide used at the rate of eight ounces per 1,000 cubic feet for a period of two hours. The cost of fumigation was approximately five cents per box in truck load lots. This treatment proved faster and less expensive than either of the two treatments - vapor heat and cold storage - used in the 1929 campaign. Fruit fly trapping, as a result of the 1956 Mediterranean Fruit Fly Campaign, became a permanent federal-state cooperative survey program in Florida.

At the peak of the program, Mediterranean fruit flies were trapped from the northern extreme, where adults were found in Seminole County on August 10, 1956, to the southern extreme, where adults were found in Key West on August 13, 1956. The final application of spray was at Sneads Island in Manatee County on February 25, 1958, and the quarantine was lifted the following day. That, to all extents and purposes, marked the end of the fight to chase the Mediterranean fruit fly out of Florida for a second time in two decades.

In the first campaign, the method of detection was not considered a complete success because the attractant used in the traps was declared weak. The McPhail trap, known as the "wet trap," could not be operated as efficiently and quickly as the plastic Steiner traps used in the later campaigns.

During the first part of the 1956 campaign, oil of Angelica seed, an expensive lure, costing average of $100 a pound, was the attractant. Later, when supplies of this oil were completely exhausted, research developed a synthetic lure called ENT 21478.

This later was improved upon and called ENT 21486. This lure proved comparable to Angelica oil and was considered more uniform and stable.

At the height of the program, 54,000 traps were in use, extending form Pensacola to Jacksonville to Key West. Records show that 11,932 medflies were trapped and identified as positive during the campaign.

The 1956 Mediterranean fruit fly infestation, which involved 28 south and central Florida counties, was eradicated on February 25, 1958, at a cost of approximately $11 million.

The 1962 Mediterranean Fruit Fly Campaign

Since the 1956 Mediterranean fruit fly eradication campaign the Florida Department of Agriculture, Division of Plant Industry, and the United States Department of Agriculture have maintained a strong fruit fly detection program in an effort to detect early infestations of economic fruit flies. This program first proved its merit on June 8, 1962, when an adult Mediterranean fruit fly was trapped in Dade County.

On June 18, 1962, a federal quarantine was placed on all fruit and vegetables being moved out of the regulated area. The quarantine originally was placed on Dade County and was later extended to include Broward and Plam Beach counties. It required that all host fruit and vegetables be either fumigated or certified before being moved, and all nursery stock within the regulated area had to be either treated or certified before being moved. The federal quarantine regulated the movement from Florida to any other state any articles that might harbor the insect. State regulations controlled movement of these articles to non-infested areas of the state.

In general, when a fly infestation was found, a quarantine zone of one mile was established. This area was known as Zone I. All host fruit or produce moved out had to be fumigated. Zone II was that area lying between the Zone I boundary and the Federal quarantine boundary. Fruit and produce in Zone II could be moved without fumigation after being certified. Eleven fumigation chambers were approved for fumigating fruit and produce (Poucher 1962-64).

The method used for eradication of the Mediterranean fruit fly in the third campaign was basically the same as the 1956 campaign. Several improvements were made with the method of pesticide application. Multi-engine planes were used throughout the operations. The size of these planes ranged from a large four-engine B-17 with a carrying capacity of 1,500 gallons to a small twin-engine Beechcraft restricted to 250 gallons. All planes were equipped with a positive cut-off valve on each

nozzle. A radio was used from the aircraft to direct the entire operation. Spotters in the field measured the swath width and used kytoons to guide the pilot.

The insecticide used was 1.2 pounds of malathion and one pint of sauce bait with enough water to compose one gallon of liquid. This material was applied at the rate of one gallon per acre. The size of the spray area in the third campaign averaged 2,400 acres for a single fly find. The spray was applied at seven-day intervals for a minimum of 56 fly-free days, and the area was re-sprayed if washed off by rain within two hours after application. Ground spray was applied around a small area at the infestation immediately following rain an in between aerial applications (Poucher 1962-64).

It was during the 1962 Mediterranean fruit fly campaign that the newly developed Mediterranean fruit fly lure, Trimedlure, was used in the plastic Steiner trap. The density of traps in Dade and Broward counties was increased to approximately 40 traps per square mile. At the time the first fruit fly was found in Dade County, 941 traps were in operation. Two weeks later 3,000 traps were being tended. The 11-month battle was ended with the announcement on May 7, 1963, that Broward and Palm Beach counties had been released from quarantine. The quarantine on Dade County had been lifted on October 23, 1962. A working force of approximately 100 men was required to eradicate the pest at an expenditure of $1 million.

The 1963 Mediterranean Fruit Fly Campaign

The fourth entrance of the Mediterranean fruit fly into Florida occurred on June 17, 1963. It was discovered again near the Miami International Airport. This marked the third time in seven years that a fruit fly infestation had been detected in Dade County. An all-out attack was launched immediately against the pest. Fruit fly trapping had been reduced prior to the detection of the fly as the third campaign was completed.

When the Mediterranean fruit fly was discovered the fourth time, 2,400 traps were being tended in Dade County. This no doubt resulted in the early detection of the infestation which greatly reduced the cost of eradication and saved the state and federal governments considerable funds. The survey and control techniques used for detection and eradication of the Mediterranean fruit fly in the fourth campaign were basically the same as the 1962 campaign. The fourth campaign ended with the lifting of the quarantine in Dade County on November 26, 1963. Eradication was achieved at a cost of $100,000.

The 1964 Mediterranean Fruit Fly Campaign

On May 20, 1964, one adult male fruit fly was caught in a

trap near Pier 3 in Miami. A quickly called conference held at the Division of Plant Industry office in Gainesville the afternoon of May 20 was attended by state and federal officials. It was decided to delay aerial spray pending the discovery of more flies. It was believed the single fly was an escapee from a merchant vessel from Hawaii which had tied up at the dock on May 18. However, fruit fly officials took no chances. Traps were immediately increased from 20 to 100 per square mile within 4 square miles of the fly find, and from 20 to 60 per square mile within a 21-square-mile area adjacent to the 4-mile area. No other fruit flies were trapped (Poucher 1962-64).

The 1964 Oriental Fruit Fly Survey

On November 15, 1964, one oriental fruit fly (*Dacus dorsalis* Hendel) was trapped at 3829 Second Avenue North in St. Petersburg, touching off an all-out survey. A total of 4,850 Steiner traps were added to the 605 traps already in the field in Pinellas County. An additional 1,000 traps were put in the field in Hillsborough County, and 200 were added in Manatee County. These Steiner traps were baited with methyl eugenol and tended until January 18, 1965, when it became apparent that there was no active infestation. The one fly trapped was considered to be a hitchhiker which escaped from a ship or plane (Poucher 1964-66).

The 1965 Caribbean Fruit Fly Survey

A housewife at 301 DeLeon Drive, Miami Springs, contacted the Florida Department of Agriculture, Division of Plant Industry office in Miami on April 23, 1965, to advise that her Surinam cherries, (*Eugenia uniflora*), were heavily infested with "worms." Larvae collected and sent to the entomology laboratory in Gainesville were identified as *Anastrepha suspensa* (Loew), commonly known as the Caribbean fruit fly.

Instructions were issued to increase trapping and observe the infestation closely. Four days later, two caribflies were caught in a McPhail trap in Miami Springs, adjacent to the Miami International Airport. More than 14,000 flies had been trapped for identification by June 30, 1965, and tens of thousands had been seen in the infested area. The Caribbean fruit fly is not considered to be a serious pest of citrus and other commercial crops moving in interstate commerce, although non-commercial crops such as calamondins (X *Citrofortunella mitis*), Surinam cherries (*Eugenia uniflora*), guavas (*Psidium guajava*), loquats (*Eriobotrya japonica*), and other tropical and subtropical fruit are severely damaged or destroyed. A public hearing was held July 1, 1965, at the Florida Citrus Mutual Auditorium in Lakeland. Among those attending were state and federal agricultural officials, and leaders of the citrus and mango industries. State and federal departments of agriculture were requested to greatly intensify research, survey, control, and eradication procedures.

An announcement was made that $1 million had been made available by the Florida State Cabinet for eradication of the caribfly. A conference was held in Miami, July 15, 1965, with state and federal plant pest eradication officials and representatives of the University of Florida agricultural research stations. After a careful review of the situation, the conference participants agreed that there was no need for an eradication program at that time because the caribfly had not attacked commercial crops. This decision to delay eradication was considered by many to be a mistake, for the Caribbean fruit fly has seriously damaged most varieties of dooryard fruit in South Florida. It has infested late varieties of commercial citrus and has caused a quarantine against fresh Florida citrus bound for Arizona, California, Texas, Hawaii, and Japan (Poucher 1964-66).

The 1967 Mediterranean Fruit Fly Survey

The first Mediterranean fruit fly (*Ceratitis capitata* (Wiedemann)) detected in the state since 1964 was trapped at Miami Beach, October 10, 1967. Intensified trapping during the months of October and November did not turn up another specimen. No control or regulatory program was established. The number of Steiner traps being operated in Dade County was increased from 3,100 to 4,767 and returned to normal levels November 27, 1967.

The 1969 Oriental Fruit Fly Survey

On December 3, 1969, a Florida Department of Agriculture inspector found a male Oriental fruit fly (*Dacus dorsalis* Hendel) in a combination lure/Steiner trap at Golden Beach in northeast Dade County. By December 17 there were 1,557 additional Steiner traps being tended within five miles around the location. All traps were baited with methyl eugenol and were operated on a weekly schedule. No additional specimens of the fly were detected; therefore, half of the traps were removed the last week of February. The remaining traps were removed by April 3, 1970. This find represented the second time the Oriental fruit fly had been trapped in Florida. The previous find was in Pinellas County on November 15, 1964 (Poucher 1968-70).

The 1972 Mexican Fruit Fly Survey

On February 23, 1972, one adult female *Anastrepha ludens* (Loew) was trapped along with 18 *Anastrepha suspensa* (Loew) in a McPhail trap placed in a grapefruit tree (*Citrus paradisi*) at 1848 Loma Linda Street, Sarasota. As a result of this find, an intensive Mexican Fruit Fly Trapping Program was initiated. Using the location of this fly find as a center point, trap areas were set up in all directions. McPhail traps were placed in preferred hosts at the rate of one trap per city block, using five torula yeast borax pellets to one pint of water as a lure. Approximately 10 percent of the traps were baited with brown

sugar and water, which were later replaced with cottonseed protein pellets. At the height of this survey program, 4,178 McPhail traps were installed in six Florida counties. In conjunction with the survey activities, host fruit was collected in order to conduct fruit fly rearing studies. Larvae and pupae recovered totaled 5,155. Subsequent trapping for adults and the rearing of collected larvae revealed no new finds of the Mexican fruit fly (Poucher 1970-72).

The 1981 Mediterranean Fruit Fly Campaign

For the first time since 1967, the Mediterranean fruit fly (*Ceratitis capitata* (Wiedemann)), sometimes referred to as the medfly, was detected in Florida. On August 4, 1981, three medflies were found in a single Jackson trap which was hanging in a dooryard calamondin (X *Citrofortunella mitis*) tree at 5018 East Columbus Boulevard in Tampa. Then on August 14, 1981, another single fly was found at 401 Bermuda Boulevard on Hookers Point, two miles southwest of the original find. These were the only medflies detected, and no larvae were found. Since the fruit fly eradication efforts of 1956 and the early 1960's, contingency plans had been drawn up for use any time fruit flies become established in Florida. With the appearance of the medfly in California, Florida's plans were updated, ground spray equipment kept in readiness, and personnel to be called in were tentatively selected. Florida's goal, in any fruit fly eradication effort, is to have ground spray applied to the infested area within 24 hours of identification of the fruit fly and aerial spraying commenced as soon as feasible, hopefully within 72 hours.

State and federal workers gathered to make final plans and to implement the eradication plan. A state and a federal worker was selected to jointly supervise each phase of the operation (survey, control, regulatory, and public relations). This system has worked well in past programs and succeeded in this campaign as well, with only a few very minor problems arising. The California medfly problem, having been in the national news for over one year, paved the way for workers in the Tampa campaign. The public, news media, and local governmental officials supported the efforts with very little disagreement. The public majority seemed to understand the importance of Florida's agriculture and the need to protect it.

A total of 66 days lapsed from the time the first flies were found until the last spray was applied. Aerial spraying was scheduled every seven days for a total of eight complete applications. During the entire control operation, no major problems were encountered. With no further fly finds, the final aerial bait spray was applied on October 8, 1981, to the downtown Tampa and Ybor City areas, completing the planned eight applications.

The quarantine which restricted the movement of host fruits and vegetables from the regulated area was lifted on November 12, 1981. A total of $1 million ($500,000 federal and $500,000 state funds) was expended on this eradication campaign (Holder 1980-82).

The 1983 Mediterranean Fruit Fly Survey

One adult female Mediterranean fruit fly (*Ceratitis capitata* (Wiedemann)) was discovered in a Jackson trap near Miami International Airport on May 31, 1983. Trap density was increased in 91-square-mile zone extending 4.5 miles out from the site where the fly was found. The survey was carried out in accordance with established USDA-State emergency program procedures. Trap density ranged from as many as 100 traps per square mile in the core area to 10 traps per square mile in the buffer zone surrounding the 81-square-mile survey area.

Trap servicing was intensified to once a week in the core area, and two-week servicing in the remaining 81-square-mile zone. Intensified trapping continued throughout July 1983, with no additional flies being trapped.

The 1984 Mediterranean Fruit Fly Campaign

Four flies suspected to be Mediterranean fruit flies were found in a Trimedlure Jackson trap at 531 SW 8th Court, Miami, on June 19, 1984. The four flies were delivered to the USDA airport inspection station, where entomologist Dick Higgins tentatively identified the specimens as Mediterranean fruit flies (*Ceratitis capitata* (Wiedemann)), one unmated female and three males. The fly specimens were then taken to Gainesville, Florida where Harold Denmark, Chief of the Division of Plant Industry Entomology Bureau, confirmed the identification.

At a staff meeting of key federal and state personnel, it was agreed to follow the medfly action plan which recently was developed and agreed upon by all citrus-producing states. It was also agreed to apply aerial bait spray as quickly as a crisis exemption could be secured from the EPA. Under normal conditions in Dade County, state and federal inspectors check some 3,146 fruit fly traps every three weeks. After the medflies were found, the number of fruit fly traps tended in Dade County was increased to 4,412. From June 19 to August 8, survey personnel found 13 flies, 12 males, and 1 unmated female in eight locations. One larva was found June 23 by a neighbor of the homeowner at the original find. She found the larva in a refrigerated orange she had picked from the infested sour orange tree (*Citrus aurantium*). This important find helped pinpoint the epicenter of the infestation. Two male medflies were found August 8 on Dodge Island in traps hanging in sea grapes (*Coccoloba uvifera*) which are nonpreferred hosts. These flies are not believed to have been

part of the infestation on the mainland, because no medfly had been found in that area for longer than one generation. The flies are believed to have been hitchhikers from one of the ships that docked at the Port of Miami on Dodge Island.

On June 20, 1984, the Florida Department of Agriculture and Consumer Services and the USDA filed a quarantine defining the exact boundaries of the regulated area. No host fruit grown in the regulated area could be shipped out. Fruit passing through or being sold in the regulated area had to be covered. To help enforce the quarantine, regulatory personnel developed emergency action orders and compliance agreements to bring regulated establishments into compliance with quarantine requirements. The quarantine area contained 460 regulated establishments, which were monitored seven days per week. The regulated establishments included 58 nurseries, 152 fruit stands, 46 plant and fruit vendors at flea markets, a farmers' market with 67 vendors, and 157 mobil vendors and lawn maintenance crews.

For rapid control of adult and larval populations, the chemical/mechanical method of control is used. This method includes foliar bait spraying, fruit stripping, soil drenching, and aerial bait spraying. With foliar bait spraying, the leaves of all host plants within a 660-foot radius (approximately four blocks) of each find are sprayed with a mixture of malathion and protein spray. Foliar bait spraying continues weekly for four weeks (one generation) after the last find. Where flies and a larva were found at the site of the initial find, all host fruit were stripped from the infested property, and only mature host fruit were stripped from properties within a 600-foot radius. Where only flies were found, mature host fruit were stripped from only the infested properties. At properties within a 600-foot radius of the larval find, the soil beneath and 12 inches beyond the drip lines of host trees were drenched three times at 14-day intervals with Diazinon 4E to kill any remaining pupae.

One of the most effective methods to stop the medfly is the aerial application of malathion and protein bait spray. Flies emerging from the pupal stage, usually in the early morning hours, are hungry for protein. They seek and feed on protein for about 48 to 72 hours before mating. Newly emerging flies are attracted to the protein bait mixture and are killed when they feed on the droplets. Aerial spraying is continued for two generations (eight weeks) after the last find. The aerial applications were conducted every five to seven days, depending on rainfall. Aerial applications continued through August 28 in a 7.5-square-mile area.

Weekly applications of malathion bait spray at 12 ounces per acre showed no adverse environmental accumulation or effects to air, soil or water (Oshima et al., 1982). A mixture of 2.4 ounces of malathion and 9.6 ounces of Nu-Lure protein bait was mixed

with water until the 91 percent malathion was at 20 percent concentration. The 1984 Miami infestation was similar to the 1980 medfly outbreak in California in that it was in a heavily populated area with dooryard hosts near major airports, seaports, and light industry. Eradication was achieved on November 2, 1984, at a cost of one million dollars.

The 1985 Mediterranean Fruit Fly Campaign

When a single Mediterranean fruit fly (*Ceratitis capitata* (Wiedemann)) is detected, such as when one female was found February 25, 1985, near the Opa Locka Airport in North Miami, the Florida Department of Agriculture, Division of Plant Industry and the USDA immediately begin a delimiting survey to determine if the fly is a lone invader or part of a breeding infestation. The detection of two or more flies signals an infestation and prompts an eradication campaign.

This is what happened 43 days into the delimiting-survey program. Two male medflies were trapped April 9, 1985, approximately 2.25 miles southwest of where the female was found. A quarantine was imposed on the 110-square-mile area surrounding both finds to prohibit movement of host material from the regulated area. The sale and display of host material within the area was regulated to prevent the possible spread of the pest. Aerial treatments of malathion and protein bait spray over the infested area were reduced from the usual eight weekly sprays to four with the introduction of sterile medflies released into the eradication program.

This eradication program marked the first time sterile medflies have been released in Florida. The release of large numbers of sterile medflies was intended to overwhelm any wild medflies which might have been present in the quarantine area, providing infertile mates for the wild flies. Mating between a sterile fly and a wild fly produces infertile eggs.

Medfly pupae were reared and shipped from the California Department of Food and Agriculture's rearing facility in Honolulu, Hawaii, to Miami International Airport five days a week. The shipments then were transported to a temporary emergence facility at Opa Locka Airport. Quality control tests were conducted to monitor various performance factors on the sterile flies received from the rearing facility in Hawaii. The rearing facility in Hawaii measured the pupal size to determine if the flies would be large enough to compete with the wild flies in mating encounters. Tests to determine the percent of flies that emerge from the pupal cases and how many of those have the ability to fly were conducted at both Hawaii and Florida facilities on each shipment. Both facilities also tested one shipment weekly for mating propensity, or how fast or how willing the flies are to mate. A stress test was conducted on 50 males

and 50 females to determine how many hours, under adverse conditions, the sterile flies could survive in the environment without food. Testing was also conducted for sex ratio, to ensure that one half of the flies were males. Each shipment of sterile pupae contained a dosimeter label which visually indicated if the pupae had been properly irradiated. A strip on the label changes from light pink to blue when exposed to gamma radiation in the range of 15 to 20 kilorads. In addition, sterility checks were made by dissection and microscopic examination of the flies to assure that all shipments had been properly irradiated. Fifty-two shipments of sterile pupae were received; each shipment contained approximately six million pupae.

The first sterile flies were released May 7, 1985. Approximately 5.5 million sterile flies were released per day, five days per week. A total of 271.75 million sterile flies were released over the 75-day period which ended in July 1985.

The sterile flies were dispersed over the quarantine area from a USDA single-engine Cessna aircraft. In addition, approximately 2.6 million sterile flies were released weekly from roving ground vehicles in the 3.5-square-mile core area of the quarantine zone.

Following sterile fly release, intensified trapping was begun to determine the effectiveness of the release program. A total of 2,649 Jackson traps were tended in the 110-square-mile quarantine area for one life cycle (30 days). No wild medflies were discovered. Eradication was declared on August 27, 1985. The total eradication cost of 1.3 million dollars was shared equally between the state and federal governments.

Early detection enhances chances of eradication of any pest. This is the aim of Florida's Fruit Fly Detection Program --- earliest possible detection of any new introduction of fruit flies and, hopefully, other introduced pests as well. As fruit fly trapping techniques were greatly improved during and after the 1956 Mediterranean Fruit Fly Campaign, it became clear that early detection meant greater savings in terms of dollars and effort spent on subsequent eradication efforts.

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CHAPTER 8

Exclusion, Detection, and Eradication of Exotic Fruit Flies in California

Robert V. Dowell

The California Department of Food and Agriculture (CDFA) is charged with preventing exotic fruit flies from becoming established in the state. This is accomplished through a three-part program of which the goals are to exclude the flies when possible, to detect infestations of the flies that have penetrated the exclusion barrier, and to eradicate these infestations as they are discovered. This paper will describe how CDFA works to meet each of these goals.

Exclusion

At the heart of the exclusion program are the 16 border stations that operate on all major roads leading into California (Figure 1). Since 1982, CDFA has strengthened these stations and now operates all of them, all day, every day of the year. The staff at the border stations inspect incoming vehicles for a wide range of prohibited items ranging from African clawed frogs to wild garlic. Preference for inspection is given to automobiles with out-of-state plates; produce trucks, boats and trailers, and recreational vehicles; although any vehicle coming through the station is subject to inspection. (Automobiles represent 89 percent of the vehicles coming through the stations.) Between 16,683,679 and 20,667,390 vehicles came through the 16 inspection stations during each of the last three years. Of these, 132,378 to 157,431 each year were denied entry or had material confiscated because they were in violation of CDFA quarantine laws (Table 1).

Twelve different fruit flies were intercepted at the inspection stations between July 1983 and June 1985 (Table 2). These flies were found in 682 lots of produce in 83/84, and 1,039 lots of produce in 84/85. The two flies most commonly intercepted are the apple maggot (368/682 and 211/1,039) and the western cherry fruit fly (290/682 and 789/1,039) (Table 2). Together they represent 96 percent of all fruit fly interceptions.

Less than 1 percent of the vehicles coming through the inspection stations had materials that were in violation of CDFA quarantine laws (Table 1).

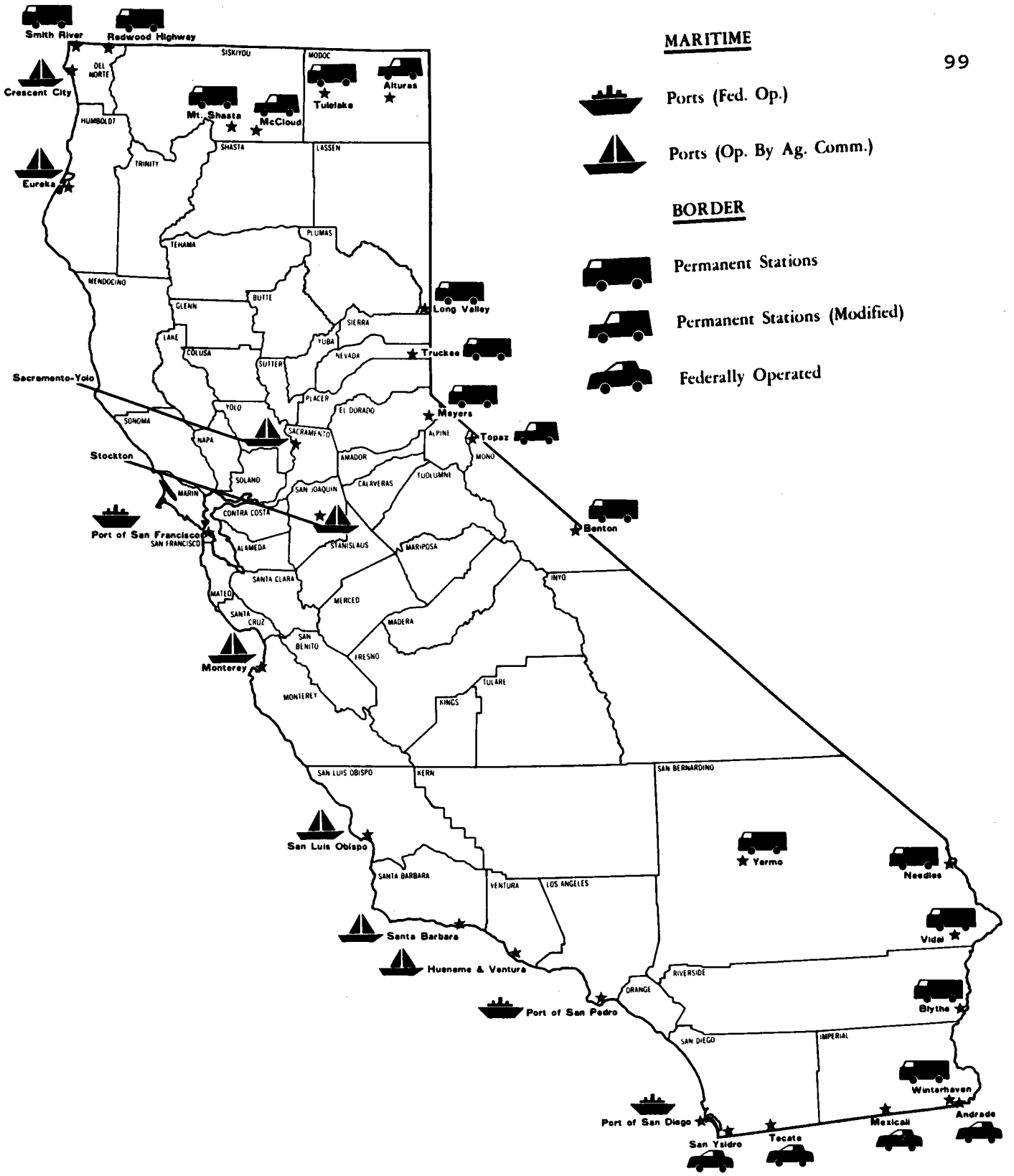

Figure 1. Border stations and port inspection points in California.

Table 1. Traffic and rejection summaries for California border stations July 1982 to June 1985.

Vehicle	Number Inspected 7/82-6/83	7/83-6/84	7/84-6/85
Automobiles	14,826,861	17,813,565	18,316,203
Trucks	1,340,090	1,692,515	1,862,102
Recreational Vehicles	516,728	630,200	489,085
Total	16,683,679	20,136,280	20,667,390
Rejections[1]	132,378	134,887	157,431

[1] Number of vehicles prevented entry into California due to infestations of serious pests or violations of plant quarantine laws.

Table 2. Summary of fruit fly interceptions at California border stations July 1983 to June 1985.

Fruit Fly	Number of Interceptions[1] 7/83 to 6/84	7/84 to 6/85
Apple Maggot	368	211
Blackcherry Fruit Fly	1	1
Blueberry Maggot	2	1
Caribbean Fruit Fly	3	2
Eastern Cherry Fruit Fly	1	1
Mexican Fruit Fly	1	11
Oriental Fruit Fly	0	1
Papaya Fruit Fly	0	1
Pepper Maggot	1	2
Walnut Husk Flies	14	19
West Indian Fruit Fly	1	0
Western Cherry Fruit Fly	290	789
Totals	682	1,039

[1] An interception represents the fruit from one vehicle and may contain numerous fruit flies.

2 Scientific names: *Rhagoletis pomenella, R. fausta, R. mendax, Anastrepha suspensa, R. cingulata, A. ludens, Dacus dorsalis, Toxotrypana curvicauda, Zonosemata electa, R. juglandis and R. sauvis, A. obliqua,* and *R. indifferens.*

Detection

CDFA maintains a statewide system of over 90,000 traps to detect fruit flies that have penetrated our exclusion barrier. The detection program is targeted at six specific fruit flies (Table 3), although most of the traps attract more than the target species. For example, the peach fruit fly can be caught in oriental fruit fly traps and the Queensland fruit fly in melon fly traps.

Trap densities vary among the areas of the state. They range from 0-3 Pherocon AM traps, 0-5 McPhail traps, 1-5 medfly, and 0-2 melon and 0-2 oriental fruit fly traps/2.56 Km2 (square mile) (Gilbert et al. 1985). Trap densities are biased towards urban areas (Table 4) for all traps except those for apple maggot. Apple maggot traps are more heavily placed in counties in northern California, and in those counties that have commercial apple orchards (Table 4). The bias toward urban counties is based upon historical data showing that only two fruit fly infestations did not occur in cities: melon fly in the 1950's and apple maggot in 1983. Since 1980, ten of eleven fruit fly infestations have occurred in urban areas of California (Table 8).

The statewide detection program has been very successful. Since 1980, nine species of fruit flies have been found in California, including three found for the first time in North America (Table 5). The lack of overlap between Tables 2 and 5 indicates that most fruit flies that establish infestations in California are not being carried into the state via roads.

The detection of one fruit fly in a trap triggers an intensive trapping program to determine if an infestation exists and, if so, to delimit it (Figure 2). No eradication program is started based upon the discovery of a single fly (Brown 1958a, b, c, d, e). The number of traps used in the delimitation survey varies based upon the dispersal ability of the target fly and the perceived attractiveness of the trap and lure (Table 6) (Gilbert et al. 1985). If the delimitation survey finds further fruit flies, an eradication program is begun.

Early detection is the key to successful eradication of fruit fly infestations. Based upon the data in Tables 5 and 8, CDFA operates a very effective detection program.

Eradication

The goal of an eradication program is to eliminate a fruit fly infestation from California. The tactics that are used vary among the fruit flies and are dependent upon the biology of the fly and what has worked before. CDFA does not view eradication as an experimental science. We prefer to use established, proven

Table 3. Summary of fruit fly traps in place for July and August 1985

Fruit Fly	Trap/lure	Number of Traps July 1985	Number of Traps August 1985
Apple Maggot	Pherocon AM®/ ammonium acetate	14,705	16,864
Caribbean and Mexican	McPhail/protein tablet	17,936	18,060
Medfly[1]	Jackson/Trimedlure	36,296	36,583
Melon Fly[1]	Jackson/Cuelure	9,302	9,683
Oriental	Jackson/methyl eugenol	9,302	9,683
Total		87,541	90,873

[1] Scientific names not listed in Table 2: *Ceratitis capitata* and *Dacus curcurbitae* respectively.

Table 4. Comparison of trap numbers in rural versus urban counties in California for August 1985

County[3]	Apple Maggots	Target Species[1] Carribbean[2]	Medfly	Melon	Oriental
Rural					
Amador	81	0	185	4	4
Madera	130	55	460	40	40
Nerced	122	0	567	42	43
Stanislaus	209	0	863	71	71
Tuolumne	97	0	171	0	0
Urban					
Alameda	607	1112	1194	124	124
Los Angeles	0	4757	4603	1473	1473
Monterey	309	181	660	140	140
Orange	0	1690	1668	911	911
San Diego	30	2179	2209	2187	2188

[1] See Table 3 for trap and lure used.

[2] Mexican fruit fly attracted to same trap.

[3] See Figure 1 for county locations.

Table 5. Fruit flies trapped or detected within California 1980-1985

Fruit Fly[5]	1980	1981	1982	1983	1984	1985[1]
Apple Maggot[4]	0	0	0	101[6]	1162[6]	170[6]
Caribbean[4]	0	0	0	1	3[6]	0
Medfly	199[6]	199[6]	2[6]	0	2	0
Melon Fly	0	0	0	0	0	2
Mexican	0	0	0	170[6]	3[6]	1
Oriental	3	3	8	14[6]	95[6]	129
Peach Fly[3,5]	0	0	0	0	2[6]	0
Solenaceous[2,3,5]	0	0	0	*	0	0
Queensland[3,5]	0	0	0	0	0	1

[1] As of December 1, 1985.

[2] Numerous larvae found in peppers sent from Hawii in 1983.

[3] First detection in North America.

[4] First detection in California.

[5] Scientific names not shown in Tables 2 and 3: *Dacus zonatus, D. latifrons,* and *D. tryoni.*

[6] Eradication program during the year.

10	10	10	10	10	10	10	10	10
10	20	20	20	20	20	20	20	10
10	20	25	25	25	25	25	20	10
10	20	25	50	50	50	25	20	10
10	20	25	50	100	50	25	20	10
10	20	25	50	50	50	25	20	10
10	20	25	25	25	25	25	20	10
10	20	20	20	20	20	20	20	10
10	10	10	10	10	10	10	10	10

Figure 2. Delimitation trap densities for medfly. Each square represents 2.56 Km^2 (1 sq. mile). Total traps = 1,700.

Table 6. Comparison of detection versus delimitation trap densities for fruit flies in California

Fly	Detection Density	Delimitation Density Core Area[3]	Adjacent Areas[4]	Total Traps[5]
Caribbean[1]	2-5	80	40	1130
Medfly	1-5	100[6]	50	1700
Melon Fly	1-2	50[6]	25	890
Oriental	1-2	5[6]	5	405

[1] Same for Mexican fruit fly.

[2] Per 2.56 Km^2 (Square mile).

[3] 2.56 Km^2 around find; represents the minimal number of traps.

[4] Adjacent 2.56 Km^2 blocks; represents the minimal number of traps.

[5] Per 207.36 Km^2 area (81 square mile).

[6] An addition 25 McPhail traps are used in the core area.

techniques. We use the least environmentally damaging option. After the problems encountered during the medfly program in 1980-1982 (Scribner 1982), we have come to realize that doing too little is the more damaging long-term tactic. Our philosophy is to do what is needed to eradicate the infestation; nothing more and nothing less.

Our desire to eradicate infestations of exotic fruit flies is based upon the belief that is it better to live without them. Dowell and Wange (1986) and Dowell (unpub. data) estimate that the fruit flies listed in Table 5 could cause crop losses of $1,110,554,000 per year with annual control costs of $311,113,000. Pesticide use is estimated to be increased by up to 7,455,000 Kg of active material per year. Dowell (1985) has estimated that up to 90 percent of these pesticides would be used by homeowners. This means that the flies on Table 5 could increase residential pesticide use by up to 6,710,000 Kg of active material/year. It is this specter of greatly increased pesticide use, especially by homeowners, that has convinced CDFA of the wisdom of living without these pests.

The tactics that have been used against infestations of various fruit flies in California range from sterile insect technique for medfly to aerial applications of malathion and bait for Mexican fruit fly, to male annihilation for oriental fruit fly (Table 7). Except for oriental fruit fly, eradication is actively pursued for two life cycles of the fly. The treatment area is then intensively trapped (Table 6) for a third life cycle. After three successive life cycles without finding any flies, eradication is declared. For oriental fruit fly, four treatments of methyl eugenol and dibrom are applied unless flies continue to be found. After the treatments cease, the area is intensively trapped until three life cycles have passed without finding a fly.

CDFA uses temperature-driven models to determine when a time period equal to two or three life cycles of the target fly have passed. Temperature probes are used to measure air and soil temperature at a depth of 2-5 cm at several sites in the treatment zone. The models are developed by CDFA staff based upon published and unpublished studies.

Since 1980, CDFA has eradicated nine separate infestations of six different fruit flies with programs against two flies at three sites still in progress as of December 1, 1985 (Table 8). It is expected that the infestations of oriental fruit fly in Santa Clara and Los Angeles counties will be eradicated by June of 1986.

Since 1980, eradication programs in California are estimated to have cost over $109,000,000. Although this seems expensive, the majority of this cost was the $100 million spent for the

Table 7. Summary of tactics used to eradicate fruit fly infestations in California 1980-1985

FLY	TACTICS
Apple Maggot	[1]Foliar sprays of phosmet
Caribbean[3]	[1]Ground sprays of malathion and bait Soil drenches of diazinon
Medfly[3]	Ground sprays of malathion and bait [1]Aerial sprays of malathion and bait Soil drenches of diazinon and fenthion Stripping of host fruit [2]Release of sterilized flies
Mexican[3]	[1]Aerial sprays of malathion and bait Soil drenches of diazinon Fruit stripping of infested and adjacent properties
Oriental	Ground sprays of malathion and bait Soil drenches of diazinon [2]Male annihilation using methyl eugenol and dibrom
Peach	[1,2]Male annihilation using methyl eugenol and dibrom

[1] Primary tactic.

[2] Preferred tactic.

[3] CDFA has contributed monies to the construction of sterile insect rearing facilities in order to have this tactic available in the future as the prferred tactic.

Table 8. Summary fruit fly eradication program in California 1980-1985

Fruit Fly	Duration[1]	Counties Involved[4]	Estimted Cost[2]
Apple Maggot	1983-present	Del Norte Humboldt Mendocino Shasta Siskiyou Trinity	$2,700,000/yr $5,700,000 to date
Caribbean	1984[3]	San Diego	$100,000
Medfly	1980-1982[3]	Alameda Contra Costa Monterey San Benito San Mateo Santa Clara Santa Cruz Stanislaus	$100,000,000
	1980[3]	Los Angeles	
	1982[3]	Los Angeles	
	1983[3]	San Joaquin	
Mexican	1983-1984[3]	Los Angeles	$3,171,000
Oriental	1983-1984[3]	San Mateo Santa Clara	 $125,000
	1984-1985[3]	Los Angeles Orange	
	1985-present	Los Angeles Orange	N/A[5]
	1985-present	Santa Clara	N/A[5]
Peach Fly	1984[3]	Los Angeles	$20,000

[1] As of December 1, 1985.

[2] Unpublished data CDFA.

[3] Successful program.

[4] See Figure 1 for county locations.

[5] Estimated at $120-150,000 total for both infestations.

medfly programs in 1980-82. CDFA views these costs as acceptable when compared to the alternative: the potential use by California homeowners of up to 6,710,000 Kg (AI)/yr of pesticide.

The Future

CDFA believes that the widespread application of pesticides is the technique of last resort to eradicate fruit fly infestations. Thus, we have contributed monies to facilities to rear Caribbean, Mediterranean and Mexican fruit flies to ensure that sterile flies are available to eradicate future infestations of these pests. We are funding research to develop better lures and traps to improve our detection programs, and we are actively investigating non-pesticidal materials for use in bait sprays.

In addition, we are strengthening and expanding our border stations and our detection trapping program. All of this is being done in an effort to ensure that the crops of California may remain free of extensive damage due to these pests.

Summary

The California Department of Food and Agriculture uses exclusion, detection, and eradication programs to keep California free of exotic fruit flies. The exclusion program utilizes 16 border stations to intercept fruit flies as they come into the state. During the last two years, 1,721 separate lots of fruit containing 12 species of fruit flies were intercepted. The detection program utilized over 90,000 traps to detect fruit fly infestations that have penetrated our exclusion program. The detection program has found nine species of fruit flies since 1980; three of which were new to North America. The eradication program is designed to eliminate the fruit fly infestations found in the detection program. Since 1980, the eradication program has succeeded in eradicating nine separate infestations of six fruit flies with three other infestations currently the object of eradication programs.

This effort is designed to prevent the large increases in pesticide use that endemic populations of these pests would cause. It is estimated that, if established, the nine species of fruit flies found since 1980 could increase residential pesticide use by up to 6,710,000 kg of active material per year.

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