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General activity and mating behavior of *Rhagoletis* flies in nature.

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GENERAL ACTIVITY AND MATING BEHAVIOR
OF RHAGOLETIS FLIES IN NATURE

A Thesis Presented

By

DAVID COURTNEY SMITH

Submitted to the Graduate School of the
University of Massachusetts in partial fulfillment
of the requirements for the degree of

MASTER OF SCIENCE

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Department of Entomology

GENERAL ACTIVITY AND MATING BEHAVIOR
OF RHAGOLETIS FLIES IN NATURE

A Thesis Presented

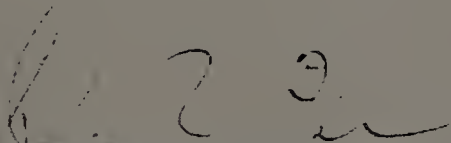
By

David Courtney Smith

Approved as to style and content by:



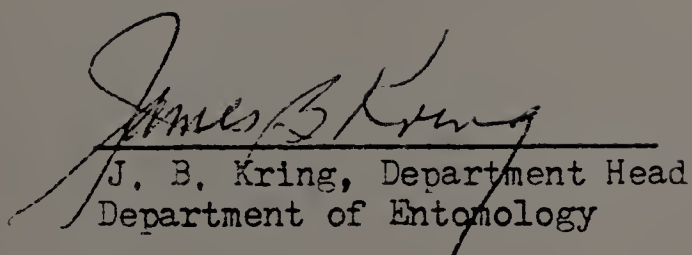
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DEDICATION

My success in this endeavor owes no small debt to the companionship of my parents and the comfort which it affords. They created an atmosphere conducive to my exploration of nature and interest in science. It is to my parents, whose love and patience and understanding nurture my aspirations, that I dedicate this thesis.

ACKNOWLEDGEMENT

I wish to express my sincere appreciation to Dr. Ronald J. Prokopy for his support, encouragement, and friendship throughout the course of this study.

I also wish to thank Mr. Chester Keffer of Monson, Massachusetts for use of his blueberry plantation.

TABLE OF CONTENTS

ACKNOWLEDGEMENT..... iv

Chapter

I. LITERATURE REVIEW..... 1

 Mating in Diptera..... 1

 Mating in Tephritidae..... 2

II. RHAGOLETIS MENDAX SEASONAL AND DIURNAL ACTIVITY..... 9

 Introduction..... 9

 Materials and Methods..... 11

 Results..... 13

 Discussion..... 25

III. RHAGOLETIS MENDAX MATING BEHAVIOR..... 29

 Introduction..... 29

 Materials and Methods..... 30

 Results..... 31

 Discussion..... 37

IV. RHAGOLETIS POMONELLA MATING BEHAVIOR..... 42

 Introduction..... 42

 Materials and Methods..... 43

 Results..... 44

 Discussion..... 48

.....

BIBLIOGRAPHY..... 53

LIST OF TABLES

1.	Location of <i>R. mendax</i> flies in nature.....	14
2.	<i>R. mendax</i> time (sec.) spent on blueberry plant parts.....	16
3.	<i>R. mendax</i> feeding and oviposition on blueberry.....	17
4.	Nature and outcome of <i>R. mendax</i> male:female encounters on blueberry.....	32
5.	Nature and outcome of <i>R. mendax</i> male:female encounters on blueberry.....	36
6.	Nature and outcome of <i>R. pomonella</i> male:female encounters observed on apple and hawthorn trees.....	45

LIST OF FIGURES

1.	Number of females observed on leaves.....	20
2.	Number of males observed on leaves.....	20
3.	Number of females observed on fruit.....	21
4.	Number of males observed on fruit.....	21
5.	Ambient temperature ($^{\circ}\text{C}$).....	22
6.	Light intensity (X1000 lux).....	22
7.	Percent of total mating pairs observed.....	23
8.	Percent of total ovipositions observed.....	23
9.	Percent of total females observed feeding.....	24
10.	Percent of total males observed feeding.....	24

CHAPTER I
LITERATURE REVIEW

Mating in Diptera

In the Diptera, mechanisms eliciting assembly of the sexes for mating appear to have evolved in several stages. According to Downes (1969), mating in flight is the ancestral condition used in most of the existing primitive families and modified in the more advanced families. Mating during aerial swarming at stations over specific, visually-recognized markers is very common among those families of Nematocera in which the male eyes and antennae are not elaborated for detecting females (Downes 1969). A swarm is a male aggregation formed when individuals independently respond to a specific marker. Even in those species of Ceratopogonidae and Culicidae which typically have large swarms, a single male may carry out a swarming flight leading to mating (Downes 1955, Provost 1958). In the biting Nematocera, females are usually captured quickly on arrival by waiting males, whose mounting responses appear to be unspecific with regard to sex or species and begin when the legs touch another fly (Downes 1958).

Several modifications of this ancestral aerial swarming habit have evolved among the higher Diptera. In some genera of Rhagionidae, males congregate on a substrate and individuals make flights only to pursue and attempt copulation with nearby flying insects

(Catts 1964,1967, Guillot et al, 1978). Mating in the Muscidae occurs on a substrate, though the male still makes a short flight or leap onto the female (Colwell and Shorey 1975, Dean et al, 1968, Tobin and Stoffolano 1973a,b). In several species of Asilidae, individual males fly between perches in search of females and, often after stereotypic courtship displays, mate on the substrate occupied by the female (Alcock 1974, Hespeneide 1978, Lavigne 1970a,b,1971,1972). Mating in the Drosophilidae often occurs after elaborate courtship displays with specific visual, auditory, and olfactory components (Spieth 1952,1974).

Mating in Tephritidae

The Tephritidae, or true fruit flies, comprise many economically important species. In most species, assembly of the sexes for mating occurs on the larval host plant. Mating occurs on the host plant but not on the part used for oviposition in Rhagoletis fausta (Osten Sacken)(Prokopy 1976), Urophora jaceana (Hering) (Varley 1947), U. solstitialis (L.), U. sirunaseva Hering, and Chaetorellia (Zwolfer 1974), Aciurina ferruginea (Doane)(Tauber and Tauber 1967), Procedidochares utilis Stone (Haseler 1965), Jamesomyia geminata (Loew)(Stoltzfus 1978), Valentibulla californica (Coquillett) and V. steyskali Foote (Wangberg 1978), Tephritis stigmatica (Coquillett)(Tauber and Toschi 1965a), Dacus tryoni (Froggatt)(Tychsen 1977), Anastrepha suspensa (Loew)

(Perdomo et al. 1976), Eurosta solidaginis (Fitch)(Uhler 1951), and Eutreta sparsa (Wiedemann)(Stoltzfus and Foote 1965). Mating occurs on host leaves or fruit in R. suavis (Loew)(Brooks 1921), R. completa Cresson (Boyce 1934), R. pomonella (Walsh)(Prokopy et al. 1971, Prokopy and Bush 1973a), Ceratitidis capitata (Wiedemann)(Feron 1962, Prokopy and Hendricks 1979), Zonosemata electa (Say)(Peterson 1923), and Z. vittigera (Coquillett)(Goeden and Ricker 1971). Phytalmia Gerstaecker flies mate on decaying logs on which females oviposit (Moulds 1977). Some tephritid species mate on plants other than those used for oviposition. D. oleae (Gmelin) and D. dorsalis Hendel mate on leaves but not necessarily on the larval host plant (Bateman 1972). D. cucurbitae Coquillett and Philophylla heraclei L. mate on nearby non-host trees which provide more food and shelter than the annual plants they use for oviposition (Nishida and Bess 1957, Leroi 1975).

Many species require a variety of nutrients beyond energy sources before sexual maturity is achieved (Bateman 1972, Christenson and Foote 1960). Few R. pomonella (Prokopy 1968), R. suavis (Brooks 1921), and C. capitata (Feron 1962) flies visit host fruit (the site of mating and oviposition) until sexually mature. D. cucurbitae females emerge from the soil beneath host plants and fly to nearby vegetation where they feed until they mature (Nishida and Bess 1957).

The age of sexual maturity varies greatly among tephritids. Mating can occur within a few hours of emergence in P. utilis (Haseler 1965) and within a day in Chaetorellia carthami Stack. (Al-Ali et al, 1979), Z. vittigera (Goeden and Ricker 1971), and Euleia fratria Loew (Tauber and Toschi 1965b). C. capitata, (Katiyar and Ramirez 1970), Gymnocarena diffusa Snow (Kamali and Schulz 1974), R. pomonella (Prokopy et al. 1972), and D. dorsalis (Roan et al. 1954) require three to ten days maturation before mating.

Males of several species, including Rioxa pornia (Walker) (Pritchard 1967), R. pomonella (Prokopy 1975), and R. cerasi L. (Katsoyannos 1976), produce volatile sex pheromones which attract females for mating. Males often congregate on leaves, release sex pheromone, and mate with attracted females in D. tryoni (Tychsen 1977), C. capitata (Ohinata et al. 1973, Prokopy and Hendricks 1979), and A. suspensa (Nation 1972, Perdomo et al. 1976). The sex pheromone of D. cucurbitae males is attractive to conspecific females and those of D. dorsalis, though the D. dorsalis male pheromone attracts only conspecific females (Kobayashi et al. 1978). D. oleae is the only reported tephritid species in which the female produces a sex pheromone attractive to males (Haniotakis 1974, 1977).

Apart from sex pheromones, some species produce substances which arrest conspecifics arriving at the site of deposition and

thus increase the frequency of sexual encounters. In R. cerasi and R. pomonella, an arrestant deposited on fruit by mature females has no effect on male arrival but causes males to spend up to twice as much time on that fruit as on unmarked fruit (Katsoyannos 1976, Prokopy and Bush 1972).

Once the sexes assemble at the mating site, visual, auditory, and gustatory courtship displays stimulate copulation in many species. Stereotypic visual displays by both sexes are characteristic of A. ferruginea, T. stigmata, and E. fratria (Tauber and Tauber 1967, Tauber and Toschi 1965a,b). A. suspensa males possess a distinct auditory pattern, produced by wing vibration, for signalling and for courting females (Webb et al. 1976). Wing vibrations also account for the male sounds which precede copulation in Anastrepha ludens (Loew) (Flitters 1964), D. tryoni (Monro 1953, Myers 1952), D. dorsalis (Roan et al. 1954), D. olea and C. capitata (Rolli 1976). Males of E. sparsa and R. pornia produce a foamy substance which may act as an aphrodisiac since the female consumes it during copulation (Stoltzfus and Foote 1965, Pritchard 1967).

Most temperate species mate under favorable conditions any time during the day. In R. pomonella (Prokopy et al. 1972), R. fausta (Prokopy 1976), R. completa (Boyce 1934), Z. vittigera, (Goeden and Ricker 1971), Z. electa (Peterson 1923), G. diffusa (Kamali and Schulz 1974), and E. solidaginis (Uhler 1951), mating

occurs during any portion of the day when incident light intensity is adequate for vision and body temperature is sufficient for flight. The tropical or subtropical species D. dorsalis (Roan et al. 1954), D. oleae (Haniotakis 1974), D. zonatus (Qureshi et al. 1974), D. tryoni (Barton Browne 1957a, Gee 1969), Pterandrus rosa (Ksh.) (Myburgh 1962), and A. ludens (Flitters 1964) mate at dusk, while C. capitata (Myburgh 1962, Prokopy and Hendrichs 1979) and D. neohumeralis (Gee 1969) mate throughout the day.

The frequency of female mating varies appreciably among tephritid flies. Females of G. diffusa (Kamali and Schulz 1974), Z. vittigera (Goeden and Ricker 1971), and R. completa (Boyce 1934) mate before each oviposition. Multiple mating is required in D. dorsalis and R. pomonella to ensure a high level of egg fertility (Christenson and Foote 1960, Neilson and McAllan 1965). The non-mating intervals of D. tryoni and D. oleae females result from deposition in the female of some male accessory gland material during copulation (Fletcher and Giannakakis 1973, Tychsen and Fletcher 1971; Tzanakakis et al. 1968). D. tryoni females are unresponsive to mating for one to four weeks after previous copulation (Barton Browne 1957b). D. oleae females lose their sexual attractiveness to males for at least six days after mating (Haniotakis 1974, Tzanakakis et al. 1968). Mating responsive-

ness of C. capitata females is negatively correlated with the volume of stored sperm in the spermathecae (Katiyar and Ramirez 1970, Nakagawa et al. 1971).

Males often appear unable to distinguish between the sexes. Mating attempts between two males occur in R. pomonella (Prokopy and Bush 1973a), R. fausta (Prokopy 1976), A. suspensa (Nation 1972), C. capitata (Feron 1962, Prokopy and Hendrichs 1979), E. fratria (Tauber and Toschi 1965b), E. solidaginis (Uhler 1951), A. ferruginea (Tauber and Tauber 1967), D. tryoni (Myers 1952, Tychsen 1977), and D. oleae (Economopoulos et al. 1971). Often as a result of these intrasexual mating attempts, two males engage in various forms of aggressive behavior involving physical contact. This behavior occurs in R. completa (Boyce 1934), R. suavis (Brooks 1921), R. pomonella (Biggs 1972, Prokopy and Bush 1973a), R. indifferens (AliNiasee 1974), C. capitata (Feron 1962, Prokopy and Hendrichs 1979), E. sparsa (Stoltzfus and Foote 1965), D. tryoni (Tychsen 1977), P. utilis (Haseler 1965), and Phytalmia (Moulds 1977).

Because males and females of most species assemble on the larval host plant, interspecific mating among the Tephritidae is probably rare, although it has been observed in nature or artificial conditions for several species (Huettel and Bush 1972, Prokopy and Bush 1973a, Zwolfer 1972, 1974). The male's

propensity for attempting copulation with flies of similar size, shape, and wing and body patterns underscores the importance of the larval host plant as a species-specific rendezvous site (Bush 1969a) maintaining the genetic integrity of the species.

CHAPTER II

RHAGOLETIS MENDAX SEASONAL AND DIURNAL ACTIVITY

Introduction

Although a considerable amount of anecdotal information has been accumulated on adult feeding, mating, and oviposition activities of higher dipterous flies in nature, few quantitatively systematic studies have been reported. Among these are quantitative studies on the predatory behavior (Hespenheide and Rubke 1977, Lavigne 1970, Scarbrough 1978) and diurnal activity and seasonal distribution of some Asilidae (Hespenheide 1978, Lavigne and Holland 1969, Scarbrough and Norden 1977), the diurnal and seasonal distribution and activity of several species of Syrphidae (Campan 1973, Maier and Waldbauer 1979a,b), and a thorough analysis of adult distribution and reproductive behavior in a species of Scatophagidae (Parker 1970a-d, 1971, 1974a).

The Tephritidae include a large number of species whose larvae feed in the flesh of growing fruits or vegetative tissues. Information on the activity of tephritid flies in nature is, for most species, largely non-quantitative and is reviewed by Christenson and Foote (1960), Bateman (1972), Boller and Prokopy (1976), and Prokopy (1977). However, some quantitative-type studies in nature have been conducted on certain species of the genus Rhagoletis, including the general activity and mating

behavior of R. pomonella (Walsh) on apple (Pyrus) (Prokopy 1975, Prokopy et al. 1971,1972, Prokopy and Bush 1972,1973a) and R. fausta (Osten Sacken) on cherry (Prunus) (Prokopy 1976).

R. mendax Curran is a major pest of blueberry (Vaccinium) in the eastern United States and Canada. Little is known about the behavior of R. mendax flies because, even after Curran (1932) described R. mendax as a distinct species, most researchers continued to consider it a host race of R. pomonella (see Christenson and Foote 1960). Hybridization experiments (McAlister and Anderson 1935, Pickett 1937, Bush and Prokopy, unpub.) show that these two species are at least partially reproductively isolated. They are karyotypically distinct (Bush 1966) and also appear to be ecologically isolated since uninfested blueberry can readily be found growing in the vicinity of infested apple or hawthorn (Crataegus) fruit, and vice versa (personal observations).

R. mendax females deposit eggs singly in ripening blueberry fruit, the flesh of which is consumed by the developing larva. The third instar larva leaves the decaying fruit, drops or crawls to the ground, and burrows 3-5 cm into soil (Lathrop and Nickels 1932) where it pupates and overwinters in diapause. In the Northeast, adult emergence from overwintering puparia usually begins during the last week of June or the first week of July, when host fruit begins to ripen. Approximately 90% of the flies emerge

within a period of 3-4 weeks and live 19-24 days (Lathrop and Nickels 1932). In the laboratory, females require 7-10 days for the ovaries to mature before oviposition begins (Prokopy, unpub.).

Here, I present the results of systematic observations of R. mendax adult activity throughout an entire season as well as a single day in mixed vegetation of high-bush blueberry, V. corymbosum, and non-host plants.

Materials and Methods

The study was conducted in Monson, Massachusetts in a plantation of cultivated high-bush blueberry (Vaccinium corymbosum), a larval host plant of R. mendax, bordered with non-host trees and shrubs. The approach taken was three-fold.

First, I recorded the location of all R. mendax adults during 40 minute periods beginning at 8 A.M., 12 Noon, and 5 P.M. (EDT) during careful and equal examination of all plant parts within 2.5 m of the ground. Cultivated blueberry bushes and all trees and shrubs within a 40m radius were examined. Data were collected on each day from July 3-26, beginning 5 days after first noted adult emergence.

Second, I charted the seasonal activity of flies on blueberry. Data collection began July 3 and ended August 15, when most fruit had dropped and the fly population was low. All

observations were made between 9 A.M. and 5 P.M. on sunny or partly sunny days on which the ambient temperature was at least 18°C at 8 A.M. Flies were selected randomly by blindly pointing at a blueberry bush and watching the fly closest to the selected spot. Flies were watched for as long as they remained in view, up to a maximum of 5 minutes. I watched each fly from approximately 30 cm away. As long as I avoided sudden movement, my presence did not appear to affect fly behavior. Fly activities were recorded verbally on tape and later transcribed for analysis.

Fly activities were defined as follows: feeding = lowering the proboscis to touch the surface on which the fly was situated; boring = insertion of the female ovipositer into a fruit; oviposition = deposition of an egg as evidenced by subsequent ovipositer dragging (Prokopy et al. 1976); a mating pair = a male and female in copula.

Third, I charted the hourly activity of flies on cultivated blueberry from 6 A.M. until 9 P.M. on July 26, which was sunny and calm. Each fly was observed for a maximum of 30 seconds. Each hour, ambient temperature in the shade was recorded with a stem thermometer and incident light intensity was measured with a Gossen Lunasix light meter, which was held at arm's length in the open and pointed directly upward.

Results

In all, 1004 of the total 1074 individual flies observed in the first part of the study were located on the cultivated blueberry bushes (Table 1). Of the remaining 70 flies, 62 were on three trees (one black oak, Quercus velutina, and two gray birches, Betula populifolia) 7m away. No flies were observed on a stand of fruiting, wild low-bush blueberry, V. angustifolium, 30m from the cultivated blueberry.

Mating pairs were observed only on cultivated blueberry (Table 1). While some flies on non-host plants occasionally moved from leaf to leaf, most were stationary on the bottom surface of leaves and none fed. Forty-three of the 70 flies on non-host plants were recorded on 3 rainy days during the 24-day data collection period. On those 3 days, most flies on blueberry and on non-host plants alike were located on the bottom surface of leaves. Over the entire study period, 22% of the 1004 flies on blueberry and 86% of the 70 on non-hosts were located on the bottom leaf surface.

The direction and destination of flights of 80 randomly selected flies of each sex was recorded on blueberry during July 10-16. Twenty-seven percent of the 124 male flights and 19% of the 383 female flights were to fruit. Of the remaining male flights, all to leaves, 64% were roughly upward and 9%

Table 1. Location of R. mendax flies in nature.*

	<u>Single male</u>	<u>Single female</u>	<u>Mating pair</u>
<u>Vaccinium corybosum</u>	521	483	36
<u>Quercus velutina</u>	20	22	0
<u>Betula populifolia</u>	6	14	0
<u>Prunus pennsylvanica</u>	0	5	0
<u>Populus grandidentata</u>	1	2	0

* July 3 - 26.

roughly downward. Of the remaining female flights, all to leaves, 53% were upward and 28% downward.

Males and females spent more time on leaves and less on fruit at the beginning of the seasonal activity period (July 3-9) than anytime later (Table 2). Although the average number of female visits to fruit progressively increased, while that to leaves changed little throughout the season, time per fruit visit substantially declined during July 29 - August 15. Throughout the season, males made relatively fewer visits to fruit and leaves than did females.

Throughout the season, 14-48% of the males spent the entire 5 minute observation period on a single fruit, but no females did so (Table 2). It appeared that fruits served as perches from which males watched for potential mates. The movement of a fly into the visual range of a perched male usually elicited a facing movement to it. If the fly landed within about 10cm, often the male walked or flew toward it to attempt copulation. The mating behavior of R. mendax is presented in Chapter III.

Feeding occurred predominately on the top surface of leaves, where females fed more often per visit than did males (Table 3). The blueberry bushes harbored many homopterans and the flies were often observed feeding on substances resembling insect honeydew. Often, 2-4 flies were observed on the same leaf feeding on bird feces. Such feces were common on the bushes during mid- and

Table 2. *R. mendax* time (sec.) spent on blueberry plant parts.

	Leaves			Fruit			Twigs			
	No. flies	No. visits	Avg. time visit [*]	No. visits	Avg. time visit	No. visits	Avg. time visit	Total time		
July 3-9	Female	205	595	72	25	328	25	16	23	155
	Male	239	167	62	88	243	119	117	3	4
July 10-16	Female	172	476	56	20	383	68	30	17	67
	Male	199	123	30	49	213	218	204	0	0
July 17-26	Female	257	671	32	12	1007	107	27	3	5
	Male	311	252	9	11	323	267	257	0	0
July 29- August 15	Female	115	316	46	17	516	73	16	0	0
	Male	104	153	18	12	105	242	239	0	0

* Maximum 300 sec.

Table 3. *R. mendax* feeding and oviposition on blueberry.

		% visits with feeding*		Fruit	
		Leaf	Fruit	% visits with boring	% visits with oviposition
July 3-9	Female	34	0	8	2
	Male	21	2	-	-
July 10-16	Female	26	1	22	15
	Male	19	4	-	-
July 17-26	Female	15	1	34	27
	Male	9	5	-	-
July 29- August 15	Female	22	7	23	19
	Male	12	4	-	-

* See Table 2 for number of visits.

late-season when ripening fruit attracted many birds. Most of the feeding done on fruit occurred late in the season when flies fed on fruit juice liberated after feeding damage by birds.

A female arriving on a fruit usually walked around the surface for 5-10 seconds, apparently searching for a suitable oviposition site. After finding one, she held her upraised body with the tip of the abdomen nearly touching the fruit surface, extended the ovipositor to the surface, and pumped the abdomen up and down several times until inserting the ovipositor through the fruit skin. Almost immediately after depositing an egg, she walked rapidly around the fruit for 5-15 seconds while dragging the extended ovipositor on the fruit surface. When finished dragging, she cleaned the ovipositor for a few seconds with the hind legs and left the fruit. Most ovipositing females spent 1-2 minutes on a single fruit. A female was never observed ovipositing more than once per visit.

Females often attempted boring into several fruits before ovipositing. Few visits to fruit resulted in boring attempts during June 3-9 (Table 3). Thereafter, the rate of attempted boring and oviposition increased. Although the ratio of oviposition to boring attempts increased throughout the season, the rate of attempted boring and oviposition decreased substantially during July 29 - August 15.

Inspection of cultivated blueberry showed that all of the 7 flies observed before dawn were motionless on the bottom surface of leaves. After dawn (ca. 5:30 A.M.), from 6-9 A.M., 45 of the 52 flies observed on the blueberry plants were on leaves (Figures 1,2), most on the top surface in the sun. From 9 A.M. - 8 P.M., 126 of the 165 females and 290 of the 312 males observed were on the fruit. Throughout the entire 15-hour daylight period, there was a highly significant positive correlation of hourly number of flies of both sexes on fruit (Figures 3,4) with (1) the hourly ambient temperature ($r = +0.928$) (Figure 5) and (2) the hourly incident light intensity ($r = +0.783$) (Figure 6). Thirty-six of 46 matings (Figure 7) and 37 of 49 ovipositions (Figure 8) occurred during the 6 hours from 12 Noon until 6 P.M. There was a highly significant positive correlation of hourly temperature and hourly light intensity with (1) mating ($r = +0.793$ and $r = +0.677$, respectively) and with (2) oviposition ($r = +0.797$ and $r = +0.765$, respectively).

Females on cultivated blueberry fed regularly throughout the day (Figure 9), but males fed mostly during the first 5 hours after dawn and the last 2 hours before dark (Figure 10). From 8-9 P.M., 8 of 15 males and all of 6 females observed were on leaves. After dark (ca. 8:50 P.M.), all 6 flies observed were on the bottom surface of leaves.

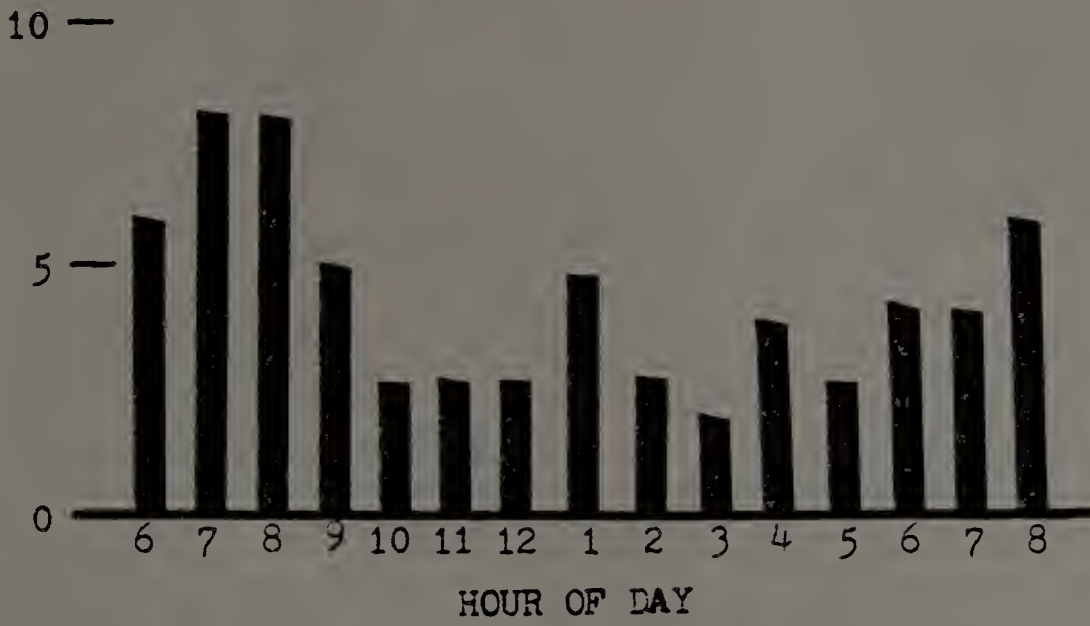


Fig. 1. Number of females observed on leaves. (Total No. 67)

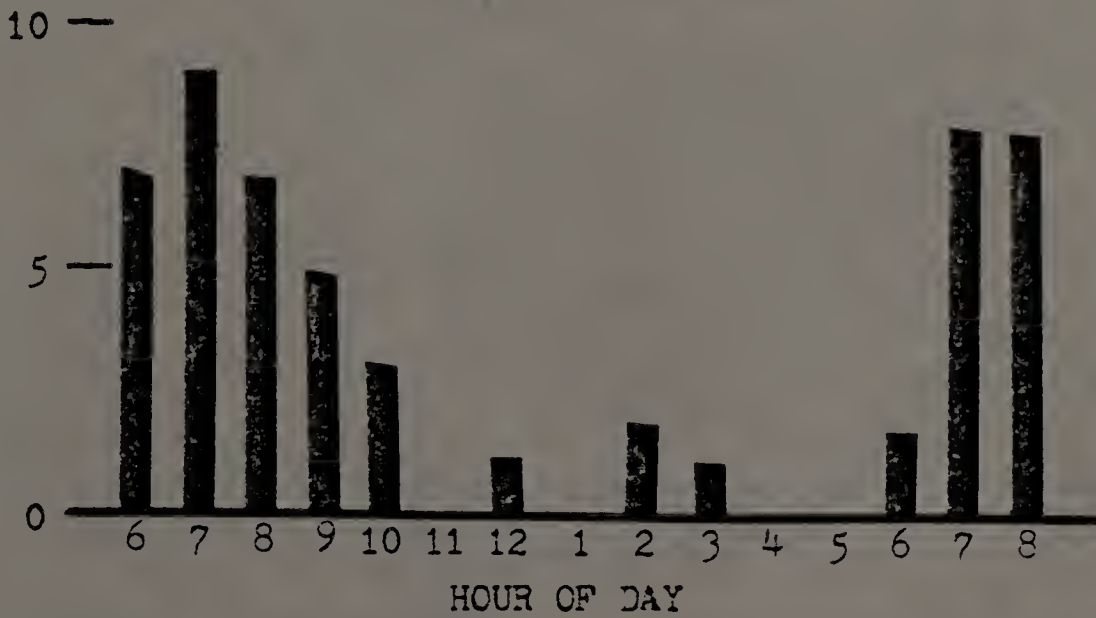


Fig. 2. Number of males observed on leaves. (Total No. 53)

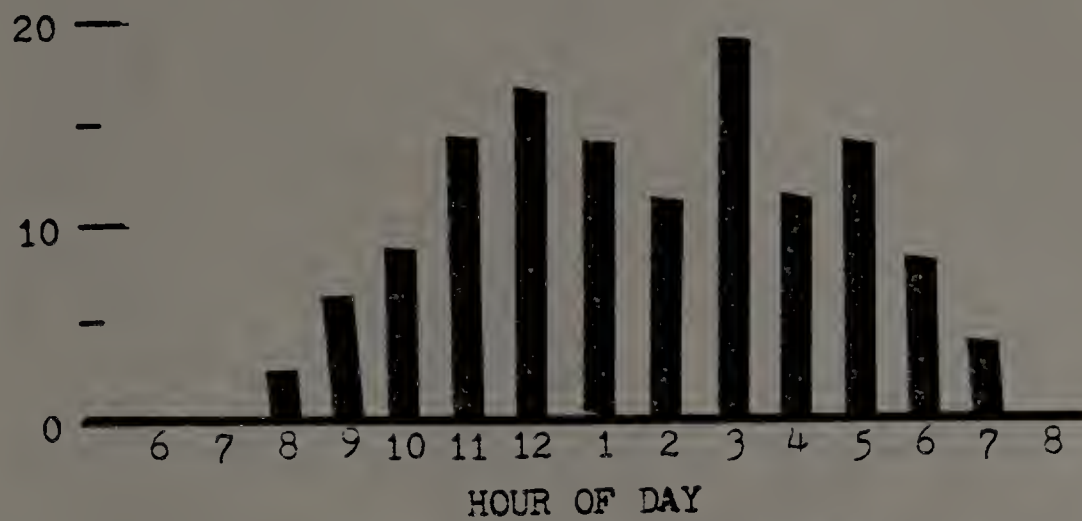


Fig. 3. Number of females observed on fruit.
(Total No. 128)

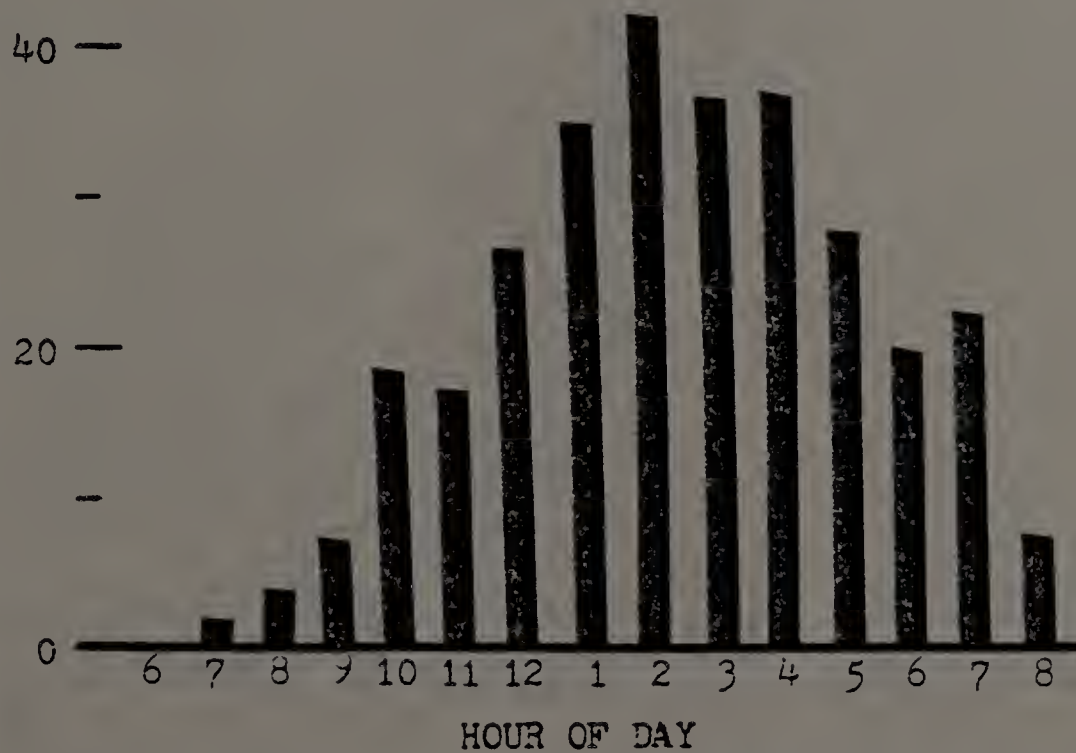


Fig. 4. Number of males observed on fruit.
(Total No. 302)

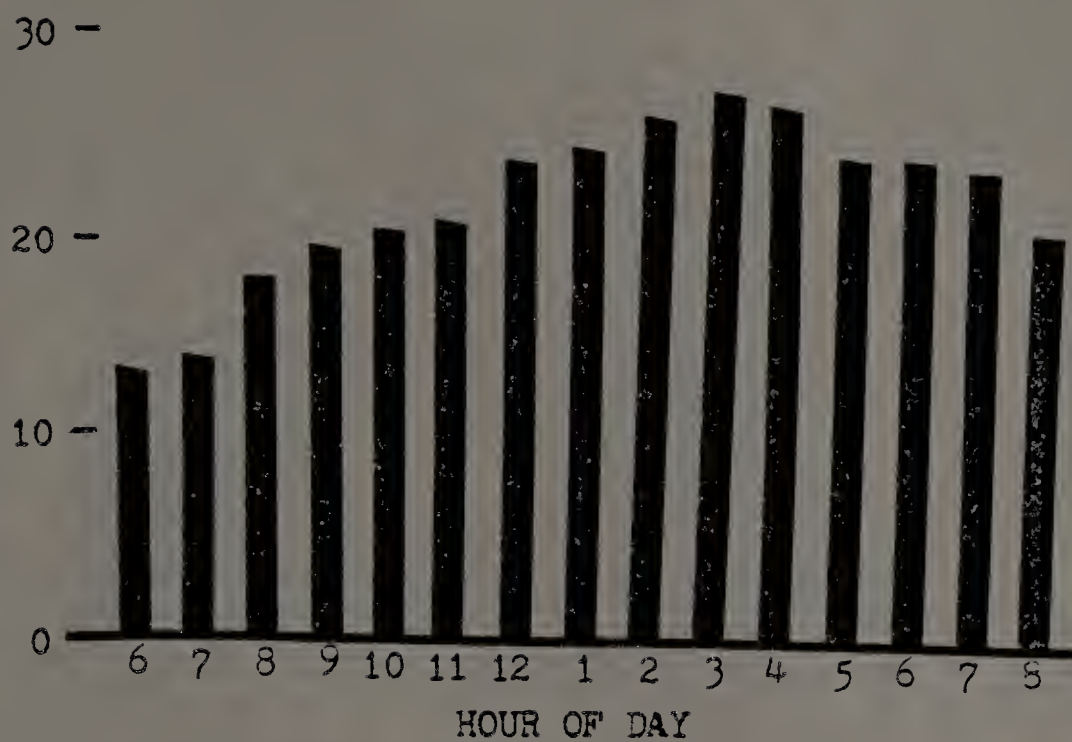


Fig. 5. Ambient temperature ($^{\circ}\text{C}$).

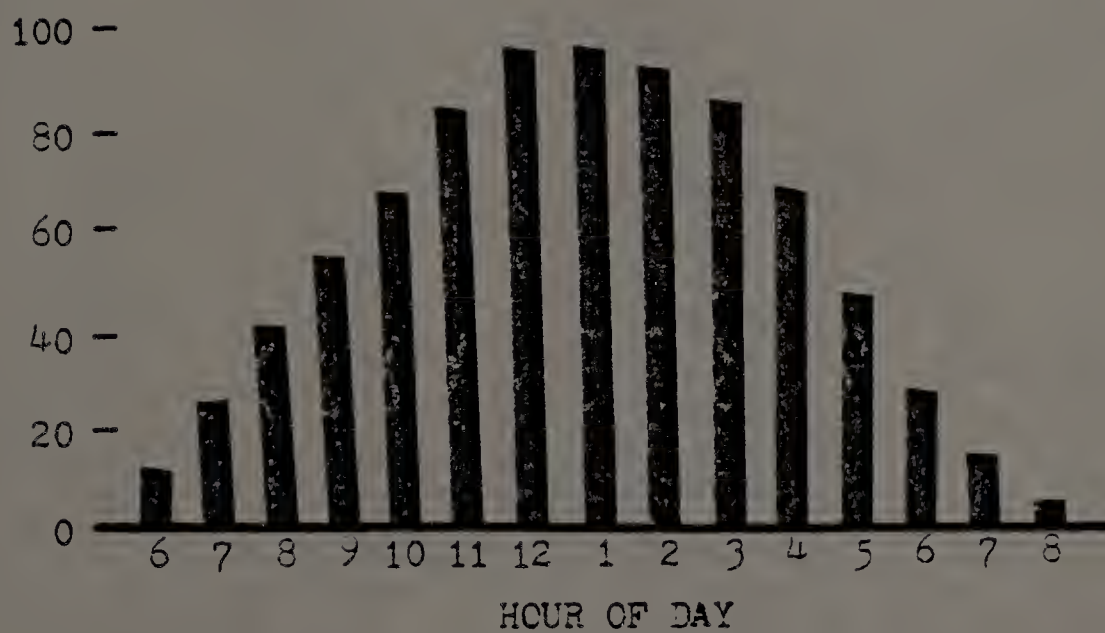


Fig. 6. Light intensity (X1000 lux).

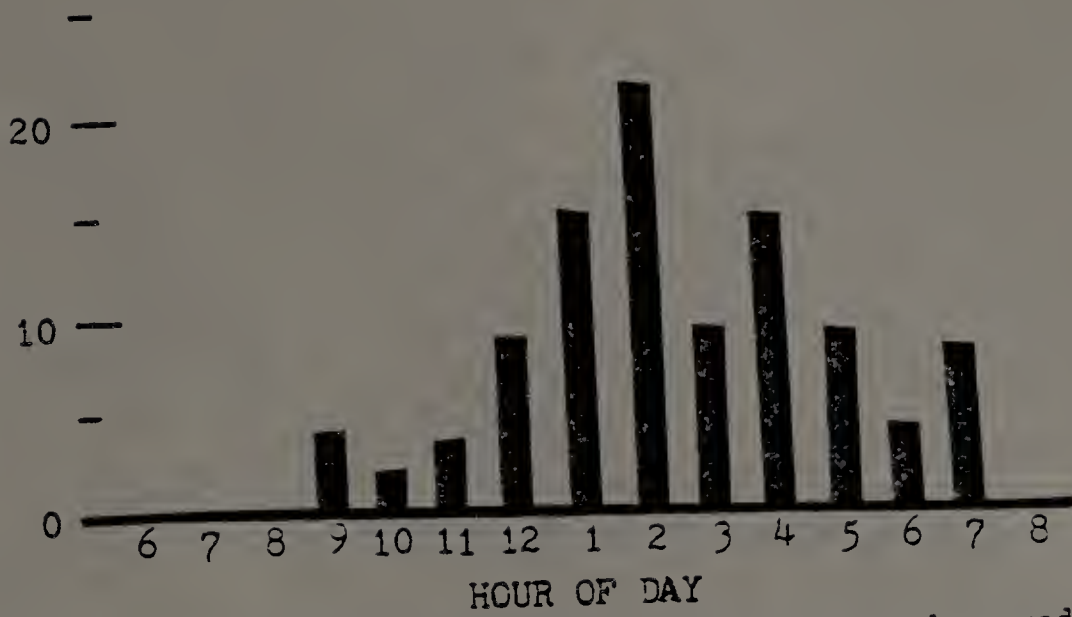


Fig. 7. Percent of total mating pairs observed.
(Total No. 46)

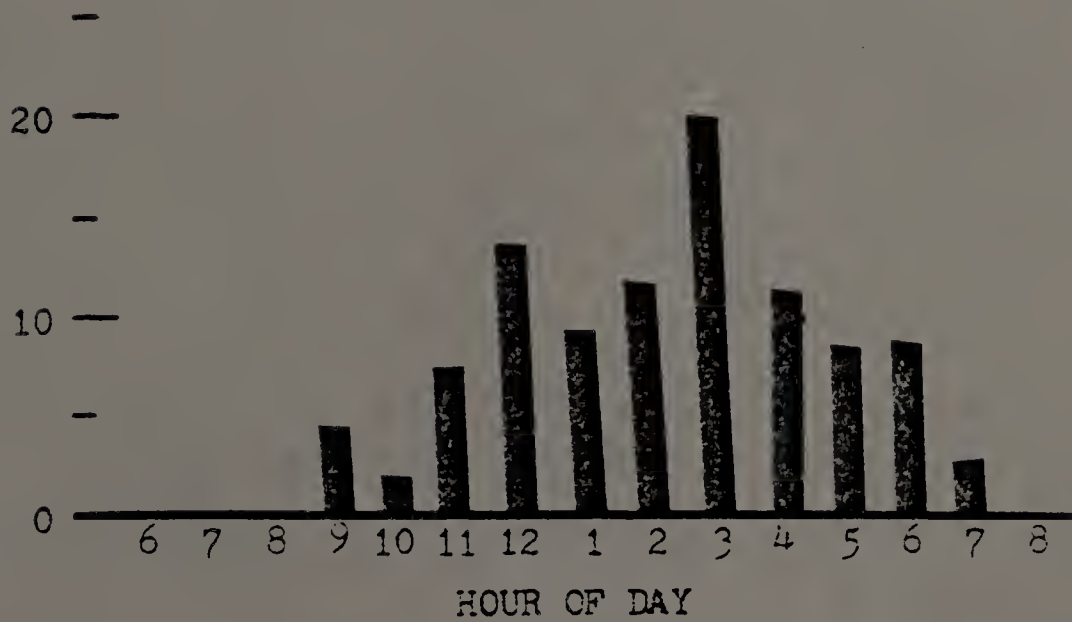


Fig. 8. Percent of total ovipositions observed.
(Total No. 49)

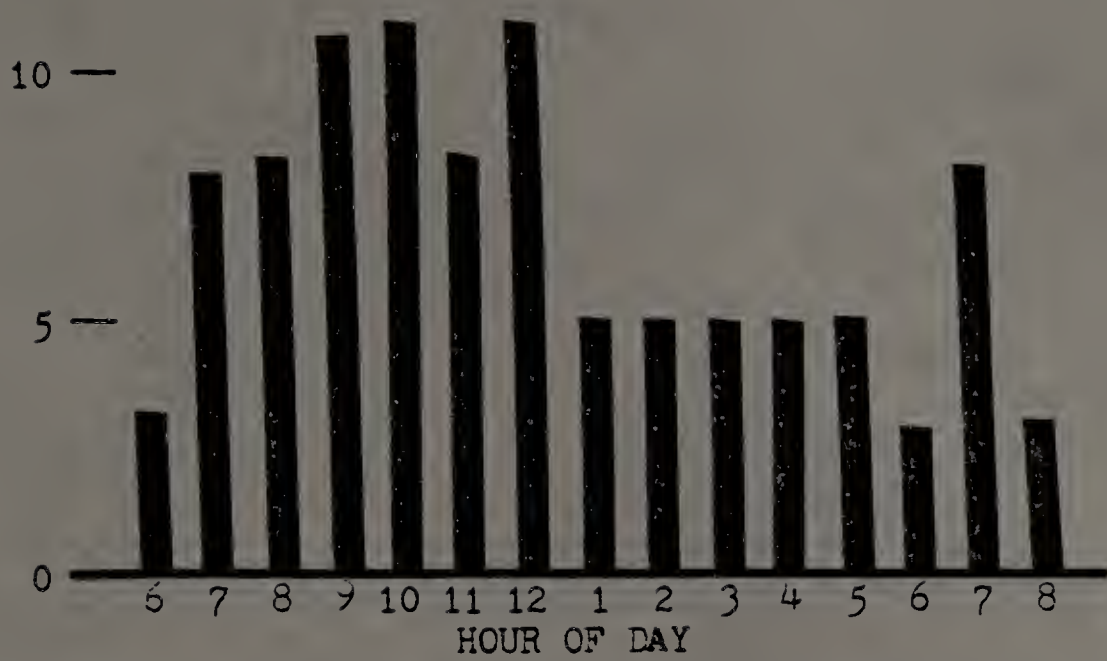


Fig. 9. Percent of total females observed feeding.
(Total No. 37)

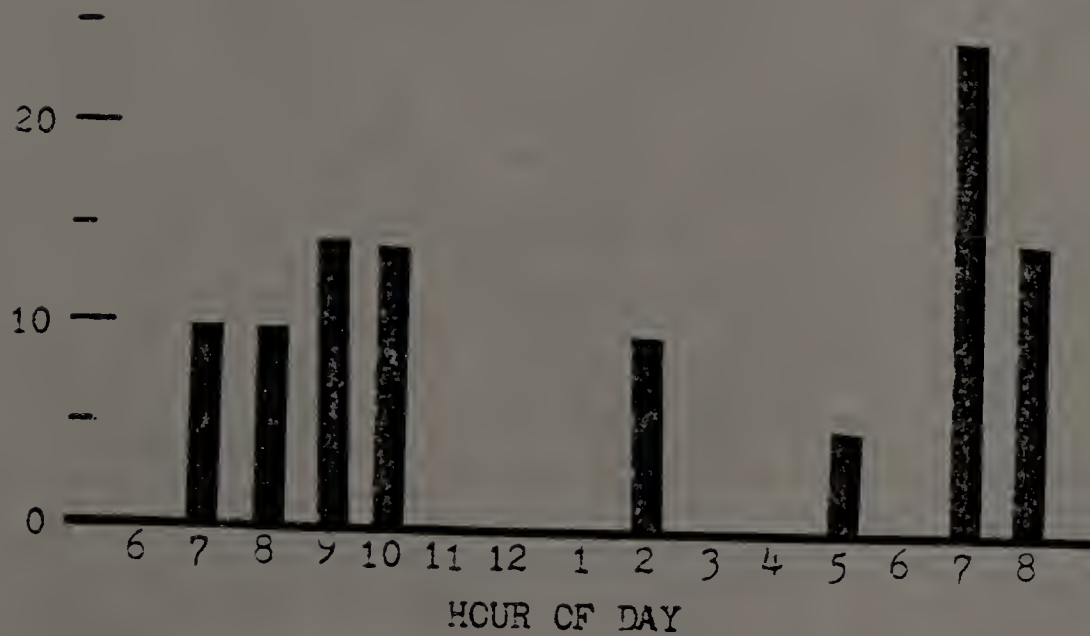


Fig. 10. Percent of total males observed feeding.
(Total No. 21)

Discussion

Most R. mendax flies were located on cultivated blueberry plants, V. corymbosum. Most flies on nearby non-host plants were located on the bottom surface of leaves and appeared inactive. Mating, oviposition, and the occurrence of both sexes on fruit were all significantly positively correlated with changes throughout the day in ambient temperature and incident light intensity. Time spent on fruit by both sexes increased as the season progressed, though the rate of boring and oviposition decreased near the season's end.

In the tephritid species Dacus zonatus Saunders, D. dorsalis Hendel, and R. fausta, flies of both sexes rest and feed on non-host plants (Syed et al., 1970, Bess and Haramoto 1961, Prokopy 1976), while D. cucurbitae Coquillett and Philophylla heraclei L. flies mate there (Nishida and Bess 1975, Leroi 1975). The biological basis for the rather common occurrence of R. mendax flies on non-host plants is unknown, since none was observed feeding or mating there. Tall, broad-leafed plants may serve as refuges from rain, since most R. mendax there were found on rainy days. However, non-host plants probably also serve as general resting sites, since the flies were found mostly on the bottom leaf surface even during sunshine. Likewise, Scatophaga sterocoraria L. flies move to shaded areas when not engaged in reproductive activities at the oviposition site (fresh cow dung) (Parker 1970a).

R. mendax mating, oviposition, and male and female visits to fruit were positively correlated with changes in light intensity and ambient temperature. Light and temperature appear to considerably affect the diurnal activity patterns of tephritid flies, as well as other insects (Lewis and Taylor 1964), in nature. For example, in Ceratitis capitata (Wiedemann), Prokopy and Hendrichs (1979) found that peak female visits to fruit and oviposition occurred during late morning to early afternoon, when light intensity and ambient temperature were greatest. Analysis of field and laboratory observations of R. pomonella led Prokopy and Bush (1972) to conclude that temperature is the principal factor affecting the daily activity pattern and that light intensity is important insofar as it is sufficient to permit adequate vision.

Although fly activity is often correlated with changes in ambient temperature, the fly's body temperature is biologically more important (Heinrich 1974). During cool (less than 20°C) morning hours, those R. mendax and R. pomonella (Prokopy and Bush 1972) flies exposed to direct sunlight would likely have a higher body temperature (owing to their largely black coloration) and could therefore be active at a lower ambient temperature than flies in the shade. Among non-tephritids, syrphid flies are able to fly at low ambient temperatures as a result of shivering and basking in the sun (Heinrich and Pantle 1975), asilids orient

themselves to be maximally insolated when ambient temperature is low (Lavigne 1971,1972), and S. stercoraria flies whose overnight resting sites are insolated in early morning become active sooner than flies resting in shaded areas (Parker 1970a). It would be adaptively advantageous to members of both sexes to become active as early in the day as possible. Early-active females would have a head start over other females in finding suitable oviposition sites, especially if those sites are limited in space or time. Likewise, early-active males would have a reproductive advantage over other males in being able to fertilize the ova of early-active females.

During the last observation period (July 29 - August 15) of R. mendax female activity on fruit, the time per visit and the percent visits with boring each decreased, while the average number of visits increased. As the season progresses, the number of uninfested fruit decreases so that females must visit more fruit before finding ones suitable for oviposition. Because males pursue females during courtship (Chapter III), the increase in male time spent on fruit throughout the season probably reflects the increase in female time spent there. According to Parker (1974b), the maintenance of maximum reproductive success should bias female time investment strategy toward feeding (i.e. toward producing a maximum number of optimal-size ova) and male strategy toward increased mate searching. These biases might explain why

(1) R. mendax females fed more often than males and (2) male feeding mostly occurred early and late in the day when females spent the least time on fruit (the predominant mating site).

The observation of R. mendax mating only on the blueberry host plants is significant. The male of most tephritid species is at least potentially polygamous. Because males generally produce more gametes than do females, the reproductive cost to a male (i.e. the loss of sperm and mate-searching time) of a subfertile mating is outweighed by the advantage accrued from seizing every opportunity for a fertile mating (Manning 1966). Interspecific mating has been observed in natural or artificial conditions for several tephritid species (Huettel and Bush 1972, Prokopy and Bush 1973a, Zwolfer 1972, 1974). The male's propensity for attempting copulation with flies of similar size, shape, and wing and body patterns underscores the importance of the larval host plant as a species-specific mating site (Bush 1969a) maintaining the genetic integrity of the species.

CHAPTER III

RHAGOLETIS MENDAX MATING BEHAVIOR

Introduction

The Tephritidae, or true fruit flies, comprise many important species. Mating usually occurs on the larval host plant (Prokopy 1977), although Dacus cucurbitae Coquillett and Philophylla heraclei L. mate on nearby non-host trees which provide more food and shelter than the annual plants they use for oviposition (Nishida and Bess 1957, Leroi 1975).

In the frugivorous genus Rhagoletis, pre-copulatory reproductive isolation is maintained in two ways. R. suavis (Loew) and R. completa Cresson both infest species of walnut (Juglans) and each possesses distinct visual characters which presumably aid in species recognition where these flies coexist (Bush 1969b). On the other hand, R. pomonella (Walsh), R. mendax Curran, R. cornivora Bush, and R. zephyria Snow, all sibling species, each infest members of a different plant family (Bush 1966). There has been no selection among them for diversity in wing and body pattern. Until the recent introduction of agricultural cultivars as new hosts, the host plant had served as a species-specific rendezvous site ensuring conspecific mating.

Although considerable quantitative information exists on the mating behavior of R. pomonella in the laboratory and in nature

(Prokopy et al. 1971, Prokopy and Bush 1973a), little is known about its sibling species. Here, I present results of a systematic observational study of the mating behavior of R. mendax flies in nature.

Materials and Methods

The study was conducted in Monson, Massachusetts in a plantation of cultivated high-bush blueberry (Vaccinium corymbosum), a principal host of R. mendax, with bordering non-host trees and shrubs. Observational data were collected for six consecutive weeks (July 3 - August 14), beginning three days after the first noted adult emergence and ending when most fruit had dropped and the fly population was low. The diurnal mating behavior of R. mendax flies was observed from 9 A.M. - 4 P.M. (Eastern Standard Time) on sunny or partly sunny days on which the temperature was at least 20°C by 9 A.M. Flies were chosen randomly by blindly pointing at a blueberry bush and watching the fly closest to the selected spot. An individual fly was watched for the duration of an encounter (until copulation) or for a maximum of 2 minutes if it did not encounter a conspecific.

Types of observed fly interactions are defined as follows:
an encounter = a meeting of two flies in which there appeared to be discernible recognition by each fly of the other's presence;
a mount = a male attempting copulation with another fly by flying or leaping onto its abdomen; and a mating = a mounting male achiev-

ing intromission with a female. Females on fruit were often engaged in various phases of oviposition-related activity which are defined as follows: pre-oviposition = a female which walked around the fruit surface apparently searching for a suitable oviposition site; oviposition = insertion of the ovipositor through the fruit skin and deposition of an egg; and post-oviposition = dragging the extended ovipositor over the fruit surface and deposition of an oviposition-detering, fruit-marking pheromone (Prokopy et al. 1976) or cleaning the extended ovipositor with the hind legs after dragging.

Results

A total of 614 male:female encounters was observed on blueberry bushes, 119 of which were on the leaves, 488 on fruit, and 7 on twigs or branches (Table 4). Thirty-five of the 38 encounters during the first week occurred on leaves. Thereafter, progressively more encounters were on fruit compared to leaves. Sixty-four percent of all encounters on leaves, but only 16% of those on fruit, occurred during the first two weeks.

All encounters on leaves occurred on the top surface, where the female was the first to arrive in 112 of the 119 cases. Typically, the male spotted her from his perch on a nearby fruit and flew to the leaf. In 61 of the 119 encounters, the male approached the female from the front, then stopped 1-3 cm away for 4-10 seconds. In 23 of these 61 cases, the female exhibited a vigorous

Table 4. Nature and outcome of *R. mendax* male:female encounters on blueberry.
 MT = mount ; TE = total encounters.

	July 3-9		July 10-16		July 17-23		July 24-30		August 1-7		August 8-14		Grand Total	
	MT	TE	MT	TE	MT	TE	MT	TE	MT	TE	MT	TE	MT	TE
<u>Site of encounter:</u>														
leaves	20	35	22	41	6	16	4	19	0	8	0	0	52	119
fruit	1	3	36	73	42	81	72	161	71	153	12	17	234	488
twigs and branches	0	0	0	2	0	0	0	4	0	1	0	0	0	7
<u>Encounters on leaves:</u>														
<u>Original occupant:</u>														
female	20	33	22	37	6	16	4	18	0	8	0	0	52	112
male	0	2	0	4	0	0	0	1	0	0	0	0	0	7
<u>Position of male relative to female:</u>														
front	16(13)	24	14(8)	23	4(1)	6	1(0)	5	0(0)	3	0(0)	0	35(22)	61
rear	2(0)	4	0(0)	2	1(0)	2	2(0)	7	0(0)	2	0(0)	0	5(0)	17
side	0(0)	1	0(0)	5	1(0)	5	0(0)	3	0(0)	1	0(0)	0	1(0)	15
other	2(1)	6	8(2)	11	0(0)	3	1(0)	4	0(0)	2	0(0)	0	11(3)	26
<u>Encounters on fruit:</u>														
<u>Original occupant:</u>														
female	1	3	34	54	38	65	68	130	63	126	12	15	216	393
male	0	0	2	19	4	16	4	31	8	27	0	2	18	95
<u>Position of male relative to female:</u>														
front	0	0	8	26	5	30	10	56	17	65	2	6	42	183
rear	1	1	16	22	21	27	43	60	43	52	6	7	130	169
side	0	2	1	6	3	8	5	16	4	17	0	0	13	49
other	0	0	11	19	13	16	14	29	7	19	4	4	49	87
<u>Female activity at MT:</u>														
pre-oviposition	0(0)	-	14(8)	-	17(7)	-	23(6)	-	21(11)	-	5(2)	-	80(34)	-
oviposition	0(0)	-	6(5)	-	13(8)	-	28(20)	-	32(27)	-	6(6)	-	85(66)	-
post-oviposition	0(0)	-	0(0)	-	2(0)	-	17(9)	-	13(8)	-	0(0)	-	32(17)	-
other	1(0)	-	16(7)	-	10(2)	-	4(0)	-	5(2)	-	1(0)	-	37(11)	-

* Number in parenthesis indicates mating.

"wing-waving" display described by Biggs (1972) for R. pomonella. In 4 cases, the male showed a similar display in response. Such a display by females, especially when combined with forward body movement, usually elicited retreat or flight of the male. Males did not attempt to mount such displaying females.

Forty-two of the 52 male:female mounts on leaves and 24 of the 25 matings there occurred during the first two weeks. Mounting on a leaf was usually preceded by the male walking toward the female and, from 1-3 cm away, making a short jump over her head and onto the abdomen. Of the 52 mounts on leaves, the male made such a frontal approach in 35 cases and a flight from a nearby fruit or leaf directly onto the female in 11 cases. Mating ensued in 22 of the former cases and 3 of the latter. No mating on leaves resulted from a rear or side approach by the male.

In encounters on fruit, the female arrived first in 393 of the 488 cases. The presence of a male on a fruit seemed to deter females from visiting that fruit, though sometimes a female did fly to a fruit already occupied by a male on the opposite side and apparently hidden from view. Shortly after arrival, the female in such cases usually engaged in pre-oviposition searching behavior, encountered the male by chance, and flew away just as he turned to face her. Mounting resulted from only 18 of 95 such encounters. In contrast, of the 393 encounters where the female was the initial fruit occupant, 216 mounts resulted from male flight from another

site onto the female's fruit or directly onto her. Thus, the male's ability to mount a female on a fruit was enhanced when the female had arrived there first.

On fruit, male approaches occurred from the front and from the rear more often than from other directions. Mounting occurred after 130 of 169 rear approaches but after only 42 of 183 frontal ones. A frontal approach usually caused the female to fly away before mounting could occur.

Mating success on fruit depended on the female's activity at the time of encounter. In 197 of the 234 mounts on fruit, the female was previously engaged in some phase of oviposition-related activity. Mating ensued in 34 of the 80 cases of female pre-oviposition behavior, in 66 of the 88 cases of oviposition, and in 17 of the 32 cases of post-oviposition behavior.

Male mating attempts often elicited active resistance from females engaged in oviposition-related activity. Such females, especially when relatively immobile during oviposition, were frequently unable to prevent mounting. A resisting female would repeatedly both lift her wings and sharply turn her body in an apparent effort to dislodge a mounted male not yet in copula. Although this was usually successful in preventing intromission, males did manage to overcome such resistance in 53 of the 132 encounters where it was observed. Once intromission was achieved, no further resistance was evident.

The mean duration of copulation for 17 mating pairs was 23 minutes (range 19-44 min). All of the 25 mating pairs on leaves remained there for at least 2 minutes. However, 107 of the 128 pairs on fruit moved to the top or bottom surface of a leaf within 2 minutes. Locomotion of mating pairs appeared to be performed solely by the female and was noticeably slower than that of a single fly. Single males were observed mounting mating pairs on leaves on 2 occasions and on fruit on 10 occasions. In 7 of these 12 cases, the pair disengaged and the female flew away.

Females encountered one another most often on fruit, though little interaction was observed. Except during early-season mating on leaves, females appeared to avoid other flies whenever possible. However, in 4 of the 23 observations of two females on the same leaf feeding on bird dung, one or both charged toward the other, causing it to fly away.

Males encountered and mounted other males (Table 5) more often than they did females. Most such encounters occurred on fruit and from a frontal approach, though mounting occurred more readily from the rear. In 68 of the 833 male:male encounters, one or both males exhibited "wing-waving", "pawing," or "boxing" behavior (Biggs 1972, Prokopy and Bush 1973a) toward the other, particularly after one had mounted and was dislodged. In 19 cases, one or both flies mounted the other several times before one flew away or both fell from the plant while struggling.

Table 5. Nature and outcome of R. mendax
male:male encounters on blueberry.
MT = mount ; TE = total encounters.

	<u>July 3 - August 14</u>	
	<u>MT</u>	<u>TE</u>
Site of encounter:		
leaves	44	63
fruit	543	752
twigs and branches	3	18
Position of approaching male relative to other male:		
front	414	603
rear	113	121
side	13	30
other	50	79

In addition to encounters directly on structures of the blueberry plant itself, males mounted females in midair very near a blueberry plant on 4 occasions. In each case, the male was perched on a fruit, spotted the female on a nearby fruit or leaf, and leaped onto her from 2-5 cm away as she flew by. None of these attempts was successful. Also, 9 mounts of males and 4 of females were observed on a fruiting pin cherry tree, Prunus pennsylvanica, 4m from the nearest blueberry bush. None was successful.

Discussion

The site of mating initiation for R. mendax flies shifted from leaves to fruit as the season progressed. Mating occurred most often on fruit, where successful copulation depended on the nature of the female's activity at the time of encounter. Only females on fruit tried to dislodge mounted males.

These sorts of observations suggest that R. mendax females engaged in oviposition-related activity on blueberry fruit were less receptive to mating than were most females on blueberry leaves. First, males usually did not succeed in mounting females after a frontal approach on fruit but did so on leaves. Most females on fruit flew away in response to a frontal approach, while most on leaves did not.

Second, male mounts on fruit resulted in mating more often when females were engaged in oviposition and post-oviposition

dragging than in pre-oviposition searching and other activities. Ovipositor extension by an essentially non-receptive female engaged in oviposition behavior may allow for some achievement of mating. Non-receptivity may arise if a female has mated recently enough so that no further insemination is required to ensure a high level of egg fertility.

Third, although female aggressive displays on leaves always appeared to discourage mounting, no effort to dislodge a mounted male was evident. However, such efforts did occur prior to intromission in many encounters on fruit. There are several possible reasons for such female resistance. Unrestricted mating may increase the chance of predation in that a mating pair is less mobile than a single fly. Although asilid flies were occasionally observed to dart after R. mendax flies, the quick flight of both precluded any observation of capture. Also, time spent copulating is lost oviposition time. Because a blueberry fruit is apparently large enough to support only one R. mendax larva to pupation (Smith and Prokopy, unpub.), females compete, as the season progresses, for an ever-dwindling supply of suitable oviposition sites. Finally, males mounting females which have just oviposited, but not yet begun or finished ovipositor dragging, may prevent adequate deposition of oviposition-deterring, fruit-marking pheromone. Should the same female, or a second one, subsequently deposit an egg in the same fruit, neither larva might survive.

We hypothesize that the mating strategy of R. mendax males shifts in response to a shift in female receptivity and activity throughout the season. Females appeared most receptive to mating early in the season while on leaves. During this period, males spent more time on leaves than they did later (Chapter II). As female time on fruit increased with increased oviposition activity, males likewise spent more time there than they did earlier. The shift of R. mendax mating site from leaves to fruit as the season progressed is consistent with that of R. pomonella on apple and hawthorn host plants (Chapter IV).

In many higher Diptera, male mating strategy depends on the probability of encountering and copulating with females at different sorts of food, oviposition, or shelter resource sites. Prokopy and Hendrichs (1979) found that males of Ceratitis capitata (Wiedemann), a subtropical tephritid, attempt copulation with females on host fruit (the oviposition site) throughout the day but on host leaves (a feeding site) mostly during late morning and early afternoon. At this time, males station themselves on the bottom surface of leaves, release sex pheromone, and mate with attracted females. Males of several species of syrphid flies locate females by patrolling flowers (food sites) during the morning and waiting in the vicinity of rot cavities of trees (oviposition sites) during afternoon (Maier and Waldbauer 1979b). This system is similar to that of the Scatophaga dung flies studied by

Parker (1970c,e,1974a). S. stercoraria L. males divide their mate-searching time between areas where incoming females land just prior to oviposition and areas (cow pats) where ovipositing females are guarded by their most recent mate against further mating by other males.

Although most pairs of R. mendax flies initiating mating on fruit moved to leaves and remained there for most of the copulatory period, most instances of supernumerary mounting occurred on fruit. Movement of mating pairs from encounter fruit to leaves may serve to preclude sexual interference by other males. Likewise, S. stercoraria mating pairs emigrate from the oviposition site during copulation to avoid such interference (Parker 1971).

Most R. mendax copulations on fruit appeared to result from males raping apparently non-receptive females engaged in certain sorts of oviposition-related activities which limited female ability to flee or resist. Although several females on fruit often did offer considerable resistance to male mating attempts, males could gain a selective advantage in courting such non-receptive females if resistance could be overcome and if the sperm could compete successfully with sperm stored in the spermathecae from a previous mating. Though little is known of sperm competition in R. mendax, sperm precedence of the most recent mating does occur in C. capitata and R. pomonella (Katiyar and Ramirez 1970, Myers et al. 1976).

R. mendax males appeared unable to distinguish between the sexes either visually or tactilly. They mounted males more often than females and sometimes continued to pursue other males even after being repeatedly dislodged from the male abdomen. Attempted copulation between two males also occurs in R. pomonella (Prokopy and Bush 1973a), R. fausta (Osten Sacken) (Prokopy 1976), and many other tephritids (see Prokopy and Bush 1973a). There are numerous examples among the Diptera of intrasexual or interspecific mating attempts where "... a sufficient frequency of appropriate matings seems to be assured only by ecological circumstances; the populations are localized and dense and the adults do not disperse (Downes 1969)." Interspecific mating has been observed in natural or artificial conditions for several tephritid species (Huettel and Bush 1972, Prokopy and Bush 1973a, Zwolfer 1972,1974). The male's propensity for attempting copulation with flies of similar size, shape, and wing and body patterns underscores the importance of the larval host plant as a species-specific rendezvous site (Bush 1969a) maintaining the genetic integrity of the species.

CHAPTER IV

RHAGOLETIS POMONELLA MATING BEHAVIOR

Introduction

The general conception of mating behavior in the frugivorous genus Rhagoletis is that fruits of host plants serve as species-specific rendezvous sites for courtship and mating (Bush 1969b). The logic of this conception is borne from an apparent intimate association between mating and oviposition behavior. During middle and late seasonal adult activity in R. suavis (Loew), R. completa Cresson, R. pomonella (Walsh), and R. indifferens Curran, initiation of successful copulation occurs almost exclusively on host fruits while the female is engaged in some phase of oviposition behavior (Brooks 1921; Boyce 1934; Prokopy et al. 1971, Prokopy and Bush 1973a; AliNiazee 1974). However, in R. fausta (Osten Sacken) all observed matings were initiated on leaves or in midair near a leaf, and most of these occurred before the onset of oviposition (Prokopy 1976). Likewise, in R. mendax Curran, a sibling species of R. pomonella, early-season mating was found to be initiated on host leaves rather than on fruits (Chapter III). In light of this recent information on R. fausta and R. mendax, it was therefore interesting to know if early-season mating in other Rhagoletis species might be initiated off the host fruit.

Here, I present the results of observations of R. pomonella sexual encounters from early- to mid-season on apple, an introduced host, and from early- to late-season on hawthorn, a native host.

Materials and Methods

I compared the relative frequency of male:female encounters, copulation attempts, and successful copulations as they were observed on various parts of 8 apple (MacIntosh and Rome) and 4 hawthorn (Crataegus spp.) trees in western Massachusetts. There were no bushes or trees of other species growing within 30m of the observation trees. Observations began about 6 days after first adult emergence from overwintering puparia beneath each host species. Emergence was first noted 21 June on apple and 9 August on hawthorn. Similarly, apple fruiting occurred earlier than hawthorn fruiting. All flies observed were selected at random as described by Prokopy et al. (1971). I collected data for 2 days during each of 4 weeks on apple (27 June - 24 July) and during each of 6 weeks on hawthorn (15 August - 25 September, at which time the population of flies had declined to a low level). The time spent watching was approximately equally divided among the 1000h-1700h on sunny days on which the ambient temperature was at least 20°C by 1000h.

Results

The data in Table 6 underscore the similarity of behavior patterns leading to encounter, attempted copulation, and successful mating between adult R. pomonella on apple and hawthorn host plants. On apple, 110 male:female encounters (= a meeting of two flies in which, to the observer, there was discernible recognition by each fly of the other's presence) were noted during the 4 week observation period, 44 of which were on leaves, 65 on fruits, and 1 on a twig. Of the 70 encounters on hawthorn in the 6 week period, 24 were on leaves and 46 on fruits.

On each host, the site of encounter shifted from the leaf, in the first half of the observation period, to the fruit thereafter. Thus, of total encounters observed during the first half, 34 of 41 on apple and 21 of 24 on hawthorn were on leaves. During the second half, 59 of the 69 encounters on apple and 43 of the 46 encounters on hawthorn were on fruits. Overall, 77% of all encounters on apple leaves and 88% of all on hawthorn leaves occurred in the first half of the observation period, while 91% of all encounters on apple fruits and 93% of all on hawthorn fruits occurred in the second half.

Most encounters began with a female as the original occupant of the encounter site and a male flying to this site from a nearby leaf or, more often, fruit. On apple and hawthorn,

Table 6. Nature and outcome of *H. pomonella* male:female encounters observed on apple and hawthorn trees.
AC = attempted copulation

	Apple - AC				Hawthorn - AC				
	27 June-10 July		11-24 July		15 August-4 September		5-25 September		Grand total
	Yes	No	Yes	No	Yes	No	Yes	No	
Site of encounter:									
leaves	22	12	34	2	8	10	24	20	44
fruit	2	4	6	32	27	59	34	31	65
twigs and branches	0	1	1	0	0	0	0	1	1
Yes No Total	22	17	39	32	27	59	58	52	110
Encounters on leaves:									
Original occupant:									
female	19	12	31	2	8	10	21	20	41
male	3	0	3	0	0	0	3	0	3
Position of male relative to female:									
front	17	(13)*	7	24	0	(-)	6	6	17
rear	2	(0)	0	2	0	(-)	0	2	2
side	2	(1)	1	3	2	(0)	4	1	5
other	1	(0)	4	5	0	(-)	2	1	6
Yes No Total	22	15	37	24	20	40	33	30	77
Encounters on fruit:									
Original occupant:									
female	1	3	4	25	16	41	26	19	45
male	1	1	2	7	11	18	8	12	20
Position of male relative to female:									
front	0	3	3	1	17	18	1	20	21
rear	2	0	2	22	0	22	24	0	24
side	0	0	0	4	3	7	4	3	7
other	0	1	1	5	7	12	5	8	13
Yes No Total	2	4	6	26	26	48	34	30	78
Female activity at AC:									
pre-oviposition	2	(2)	-	7	(3)	-	9	(5)	-
oviposition	0	(-)	-	15	(13)	-	15	(13)	-
post-oviposition	0	(-)	-	5	(2)	-	5	(2)	-
other	0	(-)	-	5	(0)	-	5	(0)	-
Yes No Total	2	0	2	27	18	45	39	38	84

* Number in () indicates number of successful copulations.

respectively, this sequence occurred in 93% and 88% of the cases on leaves, and in 69% and 76% of the cases on fruit. The percentage differences between the leaves and fruit can be explained by the tendency of females to spend much more time than males on leaves.

During the first half of the observation period, 92% (22 of 24) of all attempted copulations (= male mounting female abdomen) on apple and 100% (15 of 15) on hawthorn occurred on the leaves. During the second half, the reverse was true, with 94% (32 of 34) of the attempted copulations on apple and 100% (28 of 28) of those on hawthorn occurring on the fruit. No attempted copulations were observed on twigs or branches on either host.

The direction from which a male approached a female affected his success in attempting copulation. On leaves of apple and hawthorn, respectively, 71% and 67% of the attempted copulations were initiated from a male frontal approach. Conversely, on the fruit, only 3% and 11% were initiated from the front, with the majority (71% and 75%) initiated from a rear approach by the male. Unless a female on a fruit was in the actual process of boring with her ovipositor, anything but a rear approach by a male usually caused her to fly off.

An attempted copulation was recorded as successful if a male appeared to achieve intromission while mounted on a female's abdomen. Of all successful copulations on leaves, 13 of 14

(= 93%) on apple and 8 of 9 (= 89%) on hawthorn were preceded by a male frontal approach. Of the 34 total observations of attempted copulation on apple fruit, 29 (=85%) occurred while the female was engaged in oviposition-type behavior (searching for a suitable oviposition site, boring into the fruit with the ovipositor or, after oviposition, either cleaning the extended ovipositor with the hind legs or dragging it over the fruit surface). Of these, 20 (=69%) culminated in successful copulation. Of the 28 total observations of attempted copulation on hawthorn fruit, 26 (=93%) occurred while the female was engaged in oviposition-type behavior. Of these, 21 (=81%) culminated in successful copulation. Of the 7 encounters on fruits in which the female was not engaged in such behavior, none was so culminated.

Thus, females on leaves appeared receptive to a male frontal approach, while a male's mating success on fruits appeared more enhanced by a rear approach toward a female engaged in oviposition-type behavior. Most females so engaged appeared less receptive to male advances than most females on leaves. I considered a female to be relatively unreceptive to mating if she repeatedly resisted a male's attempts to mount her abdomen. This was done either by adopting an aggressive wing-waving display (Biggs 1972) while facing the male or by sharply turning her body several times in an apparent effort to decamp a male already mounted but not yet in copula.

Discussion

My findings show that in the early part of the mating season on apple and hawthorn host plants, R. pomonella male: female encounters and attempted copulations occurred principally on the leaves, while from mid-season onward, they occurred almost exclusively on the fruit. [This trend of mating on fruit increasing in occurrence throughout the observation period on apple is consistent with the mid-to-late season data of Prokopy et al. (1971) and Prokopy and Bush (1973a).] This seasonal difference in rendezvous site for courtship and copulation implies the existence of two different male mating strategies. The hypothetical objective of each is to decrease the search area required for locating a female.

In the first strategy, the male produces a pheromone (as yet unidentified) attractive to mature virgin females (Prokopy 1975), thereby bringing females into closer proximity to him. Among other tephritid flies, males of R. cerasi L. (Katsoyannos 1976), Anastrepha suspensa (Loew) (Nation 1972, Perdomo et al. 1976), Ceratitis capitata (Wiedemann) (Feron 1962, Ohinata et al. 1977), Rioxa pornia (Walker) (Pritchard 1967), and Dacus tryoni (Froggatt) (Barton Browne 1957b, Fletcher 1968) also produce a sex pheromone attractive to females. This same odor may conceivably function also as a courtship pheromone during

head-to-head encounters on leaves, thus facilitating virgin female acceptance of a courting male.

The second strategy stems from the likelihood that a mated female may be less attracted by male sex pheromone than might be a virgin female. Feron (1962) demonstrated that the majority of mated C. capitata females exhibit no attraction to male pheromone for at least 10 days. Similarly, Fletcher and Giannakakis (1973) showed that male pheromone of D. tryoni elicits no response in females which had mated 2 days previously. In response to a possible lack of attraction of mated females to male pheromone, the R. pomonella male apparently employs the strategy of locating an area frequented by females through detection of a female-produced male-arresting pheromone (Prokopy and Bush 1972) applied to fruits probably during some phase of oviposition behavior (Katsoyannos 1975).

Most females engaged in oviposition-type behavior appeared less receptive to male advances than most females on leaves. While it is known that R. pomonella females require multiple mating to ensure a high level of egg fertility (Neilson and McAllan 1965), it is not known how long a time, if any, must elapse before a mated female is again receptive to a male. Laboratory studies of mating frequency have been reported for several other tephritid species. D. tryoni females will not remate for at least 7 days after the initial mating (Barton

Browne 1957b), while D. dorsalis Hendel females remate at 4-5 day intervals (Christenson and Foote 1960). Most D. oleae (Gmelin) females mate only twice, usually with about 2 weeks between matings (Tzanakakis et al. 1968). Only 14-17% of C. capitata females remate within 10 days of the initial mating (Nakagawa et al. 1971). C. capitata female receptivity to repeated mating is correlated with the volume of stored sperm in the spermathecae (Nakagawa et al. 1971).

Because mature virgin R. pomonella females visit fruit and oviposit just as frequently as mated ones (Prokopy and Bush 1973b, Neilson 1975, Webster et al. 1979), not all females on fruits are necessarily less receptive to males than are virgin females on leaves. Moreover, because male pheromone may conceivably function also as an aphrodisiac, the male's ability to more closely approach a female on a fruit from the rear than from the front may render the female more receptive to mating or, especially when her ovipositor is at least partly extended, less able to resist rape. In fact, it is possible that most instances of copulation on fruits actually may have been rape by the male.

Because mature virgin R. pomonella females are attracted to males and usually offer little or no discernible resistance to copulation on leaves, it would appear that males pursuing mated (and therefore possibly less receptive) females are sacrificing potential gain of courting virgins, even if there are more mated than virgin females present. However, Parker (1970a, 1974b)

observes that a selective advantage is accrued from courting mated females if female resistance to copulation can overcome (rape) and if the sperm can successfully compete with that stored in the spermathecae from previous mating. Sperm precedence of the most recent mating does occur in R. pomonella (Myers et al., 1976).

While the two strategies employed by males for locating females may be used successively in response to female receptivity throughout the mating season, they also may be used concurrently, especially early in the season. In fact, male production of a male-arresting substance (Prokopy and Bush 1972) may play an important role in the first strategy by eliciting the formation of a lek. A lek, as defined by Emlen and Oring (1977), is "a communal display area where males congregate for the sole purpose of attracting and courting females and to which females come for mating." Male aggregations have been noted in R. mendax (Smith and Prokopy, unpub.) and in A. suspensa, whose males, as well as females, are attracted to male sex pheromone (Perdomo et al., 1976). An aggregation of males, producing more male odor than a single male, might attract a larger number of virgin females. Thus, D. tryoni males aggregate just before dusk on leaves, release pheromone, and mate there with attracted females (Tychsen 1977). C. capitata males exhibit similar behavior during late morning and early afternoon (Prokopy and Hendrichs 1979).

There are now three Rhagoletis species in which host plant foliage is the principal site of early-season mating encounters: R. pomonella, R. fausta, and R. mendax. Previous literature indicating that the host fruit is the principal site of mating initiation in R. indifferens, R. suavis, and R. completa may have involved middle to late- season observation of male rape largely unreceptive females. Perhaps if these observations had been initiated early in the mating season, they too would have revealed considerable early-season mating initiation on host leaves.

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