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Oviposition-deterring pheromone of Rhagoletis pomonella : release, residual activity, and protection of larval resources from overcrowding.

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OVIPOSITION-DETERRING PHEROMONE OF *RHAGOLETIS POMONELLA*: RELEASE, RESIDUAL ACTIVITY, AND PROTECTION OF LARVAL RESOURCES FROM OVERCROWDING

A Dissertation Presented

By

Anne Louise Averill

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ABSTRACT

OVIPOSITION-DETERRING PHEROMONE OF *RHAGOLETIS POMONELLA*: RELEASE, RESIDUAL ACTIVITY, AND PROTECTION OF LARVAL RESOURCES FROM OVERCROWDING

(May, 1985)

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Uniform spacing of eggs by ovipositing females may be adaptively advantageous in any insect species whose larvae develop at constricted sites and who have limited ability to exploit alternative sites. The apple maggot fly, *Rhagoletis pomonella* (Tephritidae), marks its egg-laying site with a pheromone that elicits dispersal of arriving conspecifics away from already occupied larval resources. This dissertation explores aspects of the oviposition-deterring pheromone (ODP) system of the apple maggot fly.

I evaluated the effect of fly or fruit treatments on quality and/or quantity of ODP released and found that fly age, fly size, and starvation influenced ODP deposition, whereas fly experience, fly diet, and presence of ODP on a fruit did not (Chapter II).

Studies of the residual activity of ODP (Chapter III) revealed that under dry conditions, the pheromone was deterrent for at least 3 weeks. A decline in pheromone activity resulted from exposure to both natural and simulated rainfall.

I began evaluation of the role of ODP as a mediator of oviposition site partitioning and as a regulator of larval competition (Chapter IV) by first establishing that the carrying capacity of Crataegus mollis hawthorns (a native host species of the apple maggot) was 1 larva/fruit. A significant decrease in larval survivorship and components of adult fitness resulted when >1 larva developed in a fruit. The amount of fruit surface marked by a female following oviposition correlated with the carrying capacity of this small host. Further, I found that ODP may need only give the first larva a headstart: in most instances, when 2 days separated introduction of 2 larvae into unpicked hawthorns capable of supporting only a single larva to pupation, the first introduced larva "won;" the second larva introduced

failed to complete development.

Finally, sampling throughout the 1.5 month hawthorn ripening season revealed an even dispersion of eggs among fruit following fruit ripening (Chapter V). It appears that ODP could be a principal mediator of this observed egg dispersion pattern in nature.

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INTRODUCTION

Identification of factors governing the abundance of animal populations has been the focus of considerable controversy for decades. Indeed, in 1859, Darwin wrote that "every single organic being around us may be said to be striving to the utmost to increase in numbers" but notes that what checks this growth is "most obscure". In the following century, discussion of this question resulted in one of the most hotly disputed debates in animal ecology. In the 1950's, two opposing points of view were developed to identify the factors important in regulating populations. On the one side, the "density independent" school (Davidson and Andrewartha 1948, Andrewartha and Birch 1954) believed that stochastic, abiotic (especially weather) factors were most critical in checking unlimited growth of populations. This view was challenged by the "density dependent" school led by Lack (1954) and Nicholson (1933), who argued that stabilizing factors such as resource (particularly food and space) shortages, and increased predator, parasitoid, or disease pressures will tend to reduce a population as it goes above a certain size.

In the following decades, many ecologists who adopted (implicitly or explicitly) the density dependent viewpoint stressed competition for resources as a dominant factor regulating a population's growth. For multispecies communities, competition was accepted as a critical process shaping community organization and differences among species requiring similar resources (MacArthur 1972, Cody and Diamond 1975, Hutchinson 1978, May 1982).

Other ecologists, particularly those studying small organisms such as insects, or organisms at lower trophic levels, have debated the importance of competition for organisms in nature (Pianka 1976). In a provocative paper on this subject, Hairston et al. (1960) asserted that for plant feeding insects, competition may be absent or rare: owing to the abundance of plant material in the world, it should be exceedingly rare for herbivore populations to reduce their plant resources to a point where competition occurs and survival and reproduction are adversely affected. Rather, such populations were thought to be more greatly influenced by predators, parasites, and weather. This view has been vigorously supported by Strong, Simberloff, and coworkers (Lawton and Strong 1981, Faeth and Simberloff 1981, Strong 1982a, 1982b; see refs. in Strong et al. 1984).

This generalized view has proven inappropriate for a number of plant-insect systems. A major challenge to this view is provided by research focused on the variability of host plants and its role in regulating insect populations. The history of the development of this line of research is reviewed by Denno and McClure (1983). In agreement with Murdoch (1966), Denno and McClure assert that variability in plant morphology, chemistry, density, or distribution limit herbivore access to and suitability of resources. Thus, although unlimited plant resources appear to be available, in many cases, only a fraction can/may be utilized by a herbivore (Whitham 1980, Stamp 1982, Benson 1978).

A second challenge to the generality of the theory advanced by Hairston et al. (1960) and Strong et al. (1984) is the finding that a growing number of insects utilize visual or chemical (oviposition deterring pheromone) cues to avoid oviposition on previously exploited resources (see refs. in Prokopy et al. 1984). Presumably, these cues serve to mediate population dispersion of individuals among available resources and decrease the probability of intraspecific encounters of immatures. The existence of such resource mediating cues strongly suggests that resources may currently be, or have been in the past, limiting. Immatures of many of the

insects that are known to utilize an oviposition-deterring pheromone (ODP) feed within constricted sites (e.g. stems, buds, or fruit) of the host and have limited or no ability to exploit alternative sites. Under such circumstances, competition for limiting resources is expected to be most immediate.

In rebutting criticisms of their 1960 paper, Hairston and his colleagues (Slobodkin et al. 1967) separate herbivores into 2 categories: those that feed on the plant itself (folivores) and those that feed on the plant's products (such as buds or fruit). Whereas these original skeptics of competition theory (as it pertains to herbivores) eventually excluded plant product consuming herbivores from their general "herbivore hypothesis," the current skeptics do not (see Strong et al. 1984).

In this dissertation, I focus on ecological aspects of the ODP system of the apple maggot fly (Rhagoletis pomonella), with particular emphasis on the role of competition. Rhagoletis pomonella females deposit ODP in a trail on the surface of a host fruit during dragging of the extended ovipositor immediately following oviposition into the fruit flesh. The larvae are constrained to develop in the host fruit selected by their mother. My initial studies focused on factors that may influence variability in ODP release on a Crataegus fruit (the

native host of R. pomonella) (Chapter II) and factors that may influence ODP residual activity in nature (Chapter III). Subsequently, I sought to establish the presence and severity of larval competition occurring in natural populations in Crataegus (Chapter IV). Finally, I evaluated a series of general hypotheses first suggested for R. pomonella by Prokopy (1972). These were (1) the area of fruit surface pheromonally marked by a female following egg-laying is related to food or space requirements of a developing larva (Chapter IV), (2) because ODP is both water soluble and only moderately stable, pheromone need only deter oviposition long enough to give the earliest developing larva a headstart, and thus, a competitive advantage over a later developing larva (Chapter IV), and (3) utilization of ODP may afford R. pomonella full exploitation of available resources (Chapter V).

C H A P T E R I I

FACTORS INFLUENCING RELEASE OF OVIPOSITION-DETERRING PHEROMONE BY *RHAGOLETIS POMONELLA* FLIES

Introduction

Studies of recruitment and sex pheromones as well as studies of oviposition-deterring pheromones (ODP) have identified numerous factors that influence pheromone release. Production of chemical recruitment trails by *Acanthomyops* and *Solenopsis* ants as well as by eastern tent caterpillars (*Malacosoma americana*) is influenced by individual assessment of food quality (Hantgartner 1969a, 1969b; Fitzgerald and Peterson 1983). These studies showed that ants produced less continuous recruitment trails and that tent caterpillars produced fewer trails following discovery of poor quality food than following discovery of high quality feeding sites. Numerous studies have demonstrated that physiological (e.g. age, mating status) and environmental factors (e.g. temperature, light) influence sex pheromone release by moths (Sanders and Lucuik 1972, Baker and Cardé 1979, Bjostad et al. 1980, Nordlund and Brady 1974), dermestid beetles (Hammack

et al. 1976), and olive fruit flies (Mazomenos 1984). Facultative ODP release has been demonstrated in the pheromone deposition behavior of the tephritid fruit fly, Anastrepha fraterculus, according to fruit size (Prokopy et al. 1982a), and Zimmerman (1980, 1982) demonstrated that Hylemya females can switch ODP release on and off, depending upon the host species being used and apparently in response to the degree of larval competition expected.

Immediately following egglaying in a host fruit, a female apple maggot fly, Rhagoletis pomonella, drags her extended ovipositor over the fruit surface and deposits a trail of ODP (Prokopy 1972). Prokopy et al. (1982c) reported that ODP, following apparent production in midgut tissue, is released into the gut contents and accumulates in the hindgut. The pheromone is released, along with other gut contents, onto the fruit during deposition of the pheromone trail.

The amount of pheromone deposited on a Crataegus hawthorn fruit (the native host of R. pomonella) determines whether females are deterred from adding additional eggs to that fruit (Chapter IV). Larvae that develop in multiply infested hawthorns may suffer detrimental effects of intraspecific competition (Chapter IV). Therefore, considerable selective advantage may be gained by females that deposit pheromone of adequate

quantity and quality to deter further egglaying upon subsequent visits to a fruit by the same or other females. I suspected that the behavior of pheromone deposition might represent a fixed action pattern that occurred without alteration (Alcock 1979), insuring sufficient pheromone deposition. Whereas the act of dragging the ovipositor following oviposition appears fixed and specific and almost always occurs (Prokopy 1972), initial lab and field observations revealed considerable variability in time spent dragging the ovipositor and in dragging bout pattern not only among females, but also among successive dragging bouts by the same female.

To elucidate factors that may influence variability in pheromone release by R. pomonella females, I set up various fruit and fly treatments and observed pheromone deposition behavior. Through measurement of the amount of pheromone trail substance deposited, and through bioassay of female response to deposited pheromone, I evaluated the quantity and quality of pheromone released, usually by individual flies, after a single ovipositional bout. Factors investigated were fly age, fly size, fly diet, starvation, fruit size and fruit quality.

Materials and Methods

Collection and maintenance methods of Rhagoletis pomonella are detailed in Prokopy (1981). Unless otherwise stated, all flies were collected as larvae from apples in nature, were mature (14-18 days old), and had no previous oviposition experience (= naive).

To quantify the amount of trail substance deposited on a fruit, newly marked fruit were dusted with dry magnetic toner, a moisture-sensitive powder used in Olivetti® copying machines. Fingerprint and talcum powders were ineffective. The magnetic toner renders the trail readily apparent because the pheromone substance is viscous and is typically a discrete, linear deposition (Fig. 1). Trail length and area were then measured microscopically with an ocular micrometer.

In these tests, the fruit of Crataegus oxyacantha 'Autumn Glory', which have a very smooth and waxy surface, were used. A fruit was attached to a dissecting probe and offered to individually caged flies in a Plexiglas-screen observation cage (15 x 15 x 15 cm). Duration of trail substance deposition was timed. Trail substance was deposited when the ovipositor was extended and dragged on

Figure 1. An oviposition-deterring pheromone trail deposited on a Crataegus hawthorn by a R. pomonella female. The trail has been dusted with Olivetti® dry magnetic toner (=xerox powder).

the fruit surface. Twenty minutes elapsed between each fruit presentation.

The length and area of trails were quantified for the following fruit or fly treatments: (1) Fly experience over time. Eleven females initially 14 days old were offered a succession of 12 hawthorns on each of 7 days; (2) Fly age. Fourteen (N = 21), 21 (N = 18) or 28 (N = 16) day old females were offered a succession of 12 hawthorns. (3) 24 hr starvation. Eighteen females provided water but no food for 24 hr and 18 females with continuous access to both food and water were offered a succession of 12 hawthorns. (4) Fruit size. Eighteen females were offered a random series of hawthorns containing six 12-13 mm diam fruit and six 18-19 mm diam fruit. (5) Pheromone marked and unmarked fruit. Twenty females were offered a random series of hawthorns containing 6 clean, unmarked fruit and 6 pheromone-marked fruit. The pheromone-marked fruit were prepared as follows: pheromone was rinsed from hawthorns used for oviposition with a known volume of distilled water. The amount of pheromone was estimated by counting the number of oviposition punctures in each washed fruit: 1 puncture = 1 dragging bout equivalent (DE). A 20 DE aliquot was applied with a cotton swab onto a 13-14 mm diam Downy hawthorn (Crataegus mollis). This amount was known to

elicit moderate levels (ca. 47%) of fruit rejection by arriving females.

For all bioassays of pheromone activity, Downy hawthorns were used. Five to eight treated and control assay fruit were hung 6-8 cm apart from the ceiling of a Plexiglas-screen (30 x 30 x 30 cm) observation cage. A single mature R. pomonella female, which had just begun oviposition in a clean fruit attached to the end of a dissecting probe, was introduced into the assay cage by placing the probe near the cage floor. The female was allowed to fly to an assay fruit overhead and subsequently allowed to visit assay fruit for up to 2 hr. Females were excluded from tests if they rejected several (ca. 6) successive clean fruit. Acceptance (attempting oviposition before leaving) or rejection (leaving without attempting oviposition) was recorded for each visit to a fruit. When a female did accept a fruit, she was, immediately following egg deposition, gently transferred to a non-assay fruit, where she commenced and completed ovipositor dragging. In this way, no assay fruit were contaminated by pheromone deposited by assay females. For each test, at least 20 females were bioassayed in this manner.

The activity of pheromone produced by flies in several treatment categories was bioassayed. (1) Fly age.

Twenty females (10-14, 20-23, or 28-30 days old) were allowed to oviposit and drag on 15 mm diam hawthorns. Because of reduced fly availability, I could not use exact-aged flies (as in the quantification of trail substance). A fruit marked by a fly from each age category plus 2 clean fruit were included in each bioassay. (2) 24 hr starvation. Females were starved as in the above starvation tests. During quantitative studies, I noticed that starved females: (a) tended to lay a maximum of only 5-6 eggs ($\bar{x}$ number of eggs = 3.8) when offered 12 successive fruit, and (b) tended to deposit more detectable trail substance during their first 2 dragging bouts than in subsequent bouts. Therefore, to test the effects of starvation on pheromone activity, I ran 2 bioassay series. In the first, I collected trails produced during the first or second dragging bouts of 15 starved females and bioassayed them in conjunction with first or second dragging bout trails of 17 unstarved females. Three fruit marked by starved females, 3 fruit marked by unstarved females, and 2 clean control fruit were included in a bioassay. In the second series, the only difference was that I collected the third, fourth or fifth dragging-bout trails of 22 starved and 19 unstarved females. (3) Fly size. Twenty-three small and 24 large females selected from a same-age group of flies that

originated from hawthorn were allowed to mark 15 mm diam C. mollis fruit. Four pheromone-marked fruit (2 each marked by a small or large fly) plus 2 clean uninfested fruit were included in a bioassay. Following bioassay, flies were oven dried for 4 hr and weighed. Mean weight (± SD) of small flies was 1.49 ± 0.16 mg and of large flies 3.48 ± 0.47 mg. (4) Fly diet. Equal-number cohorts of flies that originated from apple were fed either standard laboratory diet (a mixture of enzymatic yeast hydrolyzate and sugar, Prokopy and Boller 1970) or aphid honeydew, an important natural food of the apple maggot (Neilson and Wood 1966, Boush et al. 1969, Dean and Chapman 1973). Branches of C. mollis hawthorn trees containing vigorous colonies of aphids (species unidentified) were collected every few days and held in large buckets in a greenhouse. Honeydew was collected on glass slides under the colonies. Because it was difficult to match the quantity of the two diets, a large excess of both diets was provided from the time of fly emergence until testing. When mature (14-17 days after emergence), individual flies from each group were allowed to oviposit and drag on 16 mm diam C. mollis fruit. Fruit marked during two dragging bouts were also prepared. Bioassays were run with 2 clean control fruit plus 4 marked fruit: 2 marked during 1 or 2 dragging bouts by flies on each diet.

Because several ongoing studies in our lab (e.g. pheromone identification, electrophysiology of pheromone reception) utilized extracts prepared from fruit washings, I ran an additional test wherein pheromone drags were collected (fruit washings) from both of the diet groups and reapplied to fruit as described above. Six, 12, or 23 DE of pheromone produced by flies on either diet were swabbed onto 16 mm diam C. mollis fruit (= treatment). Bioassays were run with 6 treated fruit and 2 clean control fruit.

Results and Discussion

Variability in deposition of trail substance within and among flies

Amounts of trail substance produced by 14 day old flies offered 12 fruit in succession varied considerably, both among flies and among successive dragging bouts by the same fly (Tables 1 and 2). In the extreme cases, Fly 6 dragged for relatively short and consistent periods ($x \pm SD = 15 \pm 2$ secs), but there was less consistency in the amount of substance deposited (trail length = 17.3 ± 12.0 mm; trail area = 1.1 ± 1.1 mm^2); whereas Fly 3 exhibited longer (ca. 9x), less consistent dragging times and

deposited substantially more (ca. 6x) quantifiable substance (drag time = 127 ± 56 secs; drag length = 118.9 ± 64.3 mm; drag area = 5.9 ± 3.3 mm^2).

Variability in deposition of trail substance over time

Successive fruit marked over a day. Mean times spent dragging and pheromone deposition for each of the 12 successively offered fruit are shown in Table 3. In general, naive flies tended to deposit less trail material after the initial ovipositional bout, when several deposited no detectable material, than after succeeding bouts. Possibly, experience is necessary to produce a full pheromone trail, but this phenomenon is likely related to the physiological state of the fly: because the test females had been deprived of oviposition sites prior to testing, they tended to rapidly oviposit into and mark initially offered fruit until a reduced oviposition "drive" was realized. In subsequent bouts, there was no consistent trend of change in mean time spent dragging, trail length or area. Thus, no rapid depletion occurs in the amount of quantifiable substance deposited when flies mark a succession of 12 fruit. Because some flies lay up to 30 eggs in one day, it is possible that pheromone depletion may be noted after such numerous dragging bouts. Under laboratory conditions, however, females lay an

Table 1. Time spent during pheromone deposition (ovipositor extended and dragging on the fruit surface) and length and area of oviposition-deterring pheromone substance (= trail) deposited by two R. pomonella females offered 12 successive C. oxyacantha fruit on the same day.

	FLY 3			FLY 6		
Fruit number	Time (sec)	Trail length(mm)	Trail area(mm^2)	Time (sec)	Trail length(mm)	Trail area(mm^2)
1	63	41.5	3.8	16	0	0
2	137	76.7	4.6	14	13.4	0.4
3	121	69.9	5.9	20	38.1	3.3
4	52	48.8	7.3	14	29.2	2.0
5	183	133.6	2.9	14	9.5	0.2
6	113	46.6	2.6	15	8.0	0.2
7	151	118.0	5.8	13	2.0	0.1
8	59	169.0	7.1	15	36.6	2.2
9	212	120.5	2.6	14	23.0	3.2
10	167	264.0	13.1	16	20.5	1.1
11	134	183.5	10.7	13	16.5	1.0
12	---	155.0	4.9	13	11.1	0.9
$\bar{X}$	127	118.9	5.9	15	17.3	1.1
SD	56	64.3	3.3	2	12.0	1.1

Table 2. Mean time spent during pheromone deposition (ovipositor extended and dragging on the fruit surface) and length and area of oviposition-deterring pheromone substance (= trail) deposited by each of 12 Rhagoletis pomonella females offered 12 successive Crataegus oxyacantha fruit on the same day. Values are means ± SD.

Fly number	Time spent dragging (sec)	Trail length (mm)	Trail area (mm^2)
1	20.6 ± 5.4	29.1 ± 21.8	2.0 ± 2.2
2	37.5 ± 19.5	42.0 ± 24.5	2.2 ± 1.4
3	127.1 ± 56.3	118.9 ± 64.3	5.9 ± 3.3
4	29.2 ± 15.4	40.4 ± 19.2	1.8 ± 0.9
5	67.3 ± 23.7	53.9 ± 23.6	2.5 ± 1.3
6	15.2 ± 1.9	17.3 ± 12.0	1.1 ± 1.1
7	34.4 ± 6.3	62.0 ± 27.5	3.1 ± 1.8
8	28.5 ± 8.1	33.2 ± 18.4	2.0 ± 2.3
9	102.4 ± 36.6	101.4 ± 25.5	5.1 ± 3.7
10	23.3 ± 3.7	49.2 ± 32.8	2.4 ± 1.6
11	55.3 ± 22.2	47.5 ± 26.0	1.9 ± 1.3
12	30.2 ± 10.1	69.2 ± 21.6	3.8 ± 2.3

Table 3. Mean time spent during pheromone deposition (ovipositor extended and dragging on fruit surface) and mean length and area of oviposition-deterring pheromone substance (= trail) deposited by 12 R. pomonella females offered 12 successive C. oxyacantha fruit on the same day. Values are means ± SD.

Fruit sequence	Time spent dragging (sec)	Trail length (mm)	Trail area (mm^2)
1st	28 ± 15	24.1 ± 20.6	1.9 ± 1.7
2nd	47 ± 35	35.7 ± 33.2	2.3 ± 2.0
3rd	42 ± 24	48.2 ± 25.7	2.7 ± 2.1
4th	31 ± 14	34.4 ± 22.3	2.5 ± 2.7
5th	48 ± 48	65.2 ± 31.2	3.8 ± 2.5
6th	44 ± 26	50.5 ± 23.1	2.6 ± 1.0
7th	43 ± 39	56.7 ± 35.2	2.8 ± 1.7
8th	47 ± 20	66.5 ± 41.7	2.8 ± 1.8
9th	62 ± 59	50.9 ± 33.4	1.7 ± 1.4
10th	56 ± 43	78.3 ± 67.9	3.9 ± 3.3
11th	54 ± 25	65.7 ± 50.5	3.6 ± 3.4
12th	35 ± 19	52.1 ± 40.3	2.1 ± 1.2

average of only about 8 eggs per day over their lifetime (personal observation).

Successive fruit marked over a week. Quantitative analysis of trail deposition by flies that marked fruit over a 7 day period revealed that although mean time spent dragging per fruit was fairly consistent among days, there was some variablility in number of fruit accepted for oviposition and amount of quantifiable trail substance deposited (Table 4). For no known reason, the fewest eggs were laid on Day 3, than all other days, the most trail material was deposited on Day 4, and the least material was deposited on Day 6. There were, however, no apparent trends (e.g. decrease over time) from Day 1 to 7 for any of the measures.

Thus, the experience of a fly over a day or week does not appreciably influence the amount of pheromonal trail substance released.

Fly age

When offered a series of 12 fruit, older flies released less or less active trail substance than did younger flies (Tables 5 and 6). Although 28 day old females spent the same time dragging, they deposited significantly less trail substance (0.8-1.17 mm smaller

Table 4. Daily mean number of fruit accepted for oviposition, time spent during pheromone deposition (ovipositor extended and dragging on fruit surface), and mean length and area of oviposition deterring pheromone substance (= trail) deposited by 11 R. pomonella females offered 12 successive C. oxyacantha fruit on each of 7 consecutive days. Values are means ± SD.

Day	Number of fruit accepted	Time spent dragging (sec)	Trail length (mm)	Trail area (mm^2)
1	10.8	27 ± 11	43.9 ± 23.1	2.4 ± 2.2
2	8.9	29 ± 13	46.1 ± 29.3	2.1 ± 1.5
3	4.6	22 ± 9	43.4 ± 23.3	2.2 ± 1.4
4	9.5	26 ± 17	60.1 ± 39.9	3.1 ± 2.4
5	10.1	26 ± 16	43.3 ± 27.7	2.8 ± 2.1
6	9.4	25 ± 11	19.6 ± 12.2	1.2 ± 0.9
7	10.1	27 ± 12	37.6 ± 28.3	2.2 ± 1.9

area) in shorter trails (ca. 12-19 mm shorter) than either 14 or 21 day old females (Table 5). Because the pheromone is released, along with other gut contents, onto the fruit during deposition of the trail, the difference in trail deposition could have been due to differential food intake of young vs. old flies. Webster et al. (1979) demonstrated that food (sucrose) intake is considerably greater in 2 week old females than in 4 week old females.

The decrease (ca. 40%) in deposition of trail substance with increase in fly age (2 vs. 4 wk old) parallels results of behavioral bioassays of pheromone activity (Table 6), which show that fruit marked by 10-14 day old females were significantly less acceptable for oviposition than fruit marked by 28-30 day old flies (20% vs. 43% fruit acceptance, respectively). Fruit marked by 20-23 day old females, which were marked with ca. 30% more trail substance than fruit marked by older flies (Table 5) were less acceptable for oviposition than fruit marked by 28-30 day old flies (30% vs. 43%, respectively), but this difference was not significant. Further, there was an increase in acceptability of fruit marked by 20-23 vs. 10-14 day old females, but this was not a significant difference.

Table 5. Mean time spent during pheromone deposition (ovipositor extended and dragging on fruit surface), and mean length and area of oviposition-deterring pheromone substance (= trail) deposited by different age R. pomonella flies offered a succession of 12 C. oxyacantha fruit. Values are means ± SD.

Fly age (days)	N	Time (secs)	Trail length (mm)	Trail area (mm^2)
14	21	32 ± 20 a	47.6 ± 26.9 a	2.7 ± 2.0 a
21	18	29 ± 19 a	40.8 ± 23.1 a	2.4 ± 2.1 a
28	16	31 ± 24 a	28.4 ± 23.6 b	1.6 ± 1.1 b

Values in the same column followed by the same letter are not significantly different at the 5% level according to Student-Newman-Keul's procedure.

Table 6. Percentage of female R. pomonella accepting C. mollis fruit marked with oviposition-deterring pheromone produced by different age females. N = 20 for each age category.

Fruit treatment	Number of female arrivals on fruit treatment	% fruit acceptance
Marked by a 10-14 day old female	83	20 a
Marked by a 20-23 day old female	105	30 ab
Marked by a 28-30 day old female	116	43 b
Clean control	156	63 c

Values in the same column followed by the same letter are not significantly different at the 5% level according to a G test

Starvation

Twenty-four hr starvation severely reduced the mean number of eggs laid as well as the amount of trail substance deposited (Table 7). When offered 12 successive hawthorns for oviposition, starved females accepted fewer of these than unstarved females (3.8 and 10.7 mean fruit, respectively). Further, although starved flies spent approximately the same mean time dragging their ovipositors as unstarved flies (18 and 17 secs, respectively), starved flies deposited significantly shorter trails (ca. 22 mm shorter) of smaller area (ca. 2 mm^2 smaller). Trails produced by starved flies were typically less than half as long as those of unstarved females. Additionally, unlike successive trails produced by unstarved females, for starved females, the amount of trail substance, y, deposited following successive ovipositional bouts, x, decreased rapidly ($Y = 23.7 - 5.77X$). Following a fly's initial two dragging bouts, less or no substance was detected in many subsequent trails, with the majority of trails being very fine and barely perceptible. This result is explained by dissections of starved flies: within 24 hr of food deprivation, considerable gut content depletion had occurred.

Table 7. Mean number of clean fruit accepted for oviposition, time spent during pheromone deposition (ovipositor extended and dragging on fruit surface), and mean length and area of oviposition-deterring pheromone substance (= trail) deposited by starved (N = 18) and unstarved (N = 18) *R. pomonella* flies offered 12 successive *C. oxyacantha* fruit. Values are means ± SD.

Treatment	Number of fruit accepted	Time spent dragging (sec)	Trail length (mm)	Trail area (mm^2)
Starved	3.8 a	18 ± 10 a	10.4 ± 9.4 a	0.5 ± 0.6 a
Unstarved	10.7 b	17 ± 10 a	32.6 ± 20.1 b	2.5 ± 1.8 b

Values in the same column followed by the same letter are not significantly different at the 1% level according to a t-test.

Behavioral bioassays of comparative activity of pheromone produced by starved and unstarved flies showed poor correspondence to trail measurement results. In the first bioassay series where I collected pheromone deposited following the first two ovipositional bouts, there was no significant difference in percent acceptance of fruit marked with pheromone drags of starved flies (N = 15) vs. unstarved flies (N = 17) (50% vs. 45% acceptance, respectively) (Table 8), even though quantitative trail measurement results indicated that starved flies deposited only about 1/2 as much trail substance during these dragging bouts. In the second bioassay series, where I collected pheromone deposited following the third, fourth, or fifth ovipositional bouts, fruit marked by starved females (N = 22) were significantly less acceptable to ovipositing females than fruit marked by unstarved females (N = 19) (18% vs. 29% fruit acceptance, respectively) (Table 8). This is a surprising result because quantitative trail measurement results indicated that starved flies deposited only ca. 1/10 as much trail substance during these dragging bouts as unstarved flies. It is possible that, by reducing gut contents, the effect of starvation may have been to concentrate the pheromone, resulting in a less dilute, more deterrent deposit that was not assessable using a quantitative trail measurement

Table 8. Percentage of female R. pomonella accepting fruit marked with oviposition-deterring pheromone produced by starved or unstarved R. pomonella females following their first-second or third-fifth ovipositional bouts.

Fruit treatment	1st or 2nd bouts		3rd-5th bouts	
	Number of ♀ + arrivals	% fruit acceptance	Number of ♀ + arrivals	% fruit acceptance
Marked by a starved female	52	50 a	127	18 a
Marked by an unstarved female	64	45 a	138	29 b
Clean control	28	75 b	96	66 c

Values in the same column followed by the same letter are not significantly different at the 5% level according to a G test

technique. Interestingly, because starvation results in oocyte resorption in many Diptera (Chapman 1969), if such were the case in R. pomonella, it would be advantageous for a starving female to produce a highly deterrent pheromone deposition, and thus, maximally protect each of her few remaining eggs.

This lack of correspondence between quantitative trail measurement and behavioral bioassay results demonstrates that for any fly treatment that reduces gut contents, evaluation of R. pomonella pheromone release using a trail measuring technique may be misleading. Therefore, trail measurement must be used in conjunction with other techniques, or owing to labor intensity, be eliminated altogether.

Fly size

Behavioral bioassays revealed that small females deposited pheromone of either decreased quality or quantity as compared to larger conspecifics (Table 9). A significantly greater proportion of female visits resulted in acceptance of fruit marked once by small females (50%) as compared to fruit marked once by large females (31%). This occurred in spite of the fact that small females spent approximately the same time engaged in fruit marking (31 secs) and completed the same number of dragging

Table 9. Percentage of female R. pomonella accepting C. mollis fruit marked during a single dragging bout with oviposition deterring pheromone produced by a large (N = 24) or small (N = 23) R. pomonella female.

Fruit treatment	Number of female arrivals on fruit treatment	% fruit acceptance
Marked by a large female	167	31 a
Marked by a small female	123	50 b
Clean control	135	65 c

Values in the same column followed by the same letter are not significantly different at the 5% level according to a G test

circles (2.4) per fruit as did large females, which spent 33 secs and completed 2.5 circles. (A dragging circle is a distance dragged by a female that approximates the circumference of the fruit and is estimated by eye). Because reduction in adult size may result from intraspecific larval competition in small hawthorn hosts (Chapter IV), these results suggest an intriguing effect of overcrowding on subsequent adult fitness: a small female's decreased ability to pheromonally protect egglaying sites may lead to additional infestation by that same female or subsequently arriving females. As a result, her progeny may more likely suffer reduced larval survivorship or stunted development (Chapter IV).

Quiring and McNeil (1984c) have likewise demonstrated that small alfalfa blotch leafminer (Agromyza frontella) females produce an ODP that is less effective than that produced by large females.

Fly diet

Females fed either the laboratory diet or the honeydew diet produced equally active pheromone trails (Table 10). Bioassays wherein aqueous extracts of ODP deposited by honeydew or lab. diet fed flies were applied to fruit revealed no statistical differences between pairs of any of the concentrations tested (Table 10).

Table 10. Percentage of female R. pomonella accepting C. mollis fruit: (Test A) marked once or twice with oviposition-deterring pheromone produced by R. pomonella females fed laboratory or honeydew diet or (Test B) swabbed with an aqueous solution of 6, 12, or 23 dragging bout equivalents (DE) of pheromone collected from flies fed either diet.

Fruit treatment	Number of female arrivals on fruit treatment	% fruit acceptance
	TEST A	
Marked once by a female fed honeydew diet	128	43 a
Marked once by a female fed laboratory diet	136	42 a
Marked twice by a female fed honeydew diet	137	32 b
Marked twice by a female fed laboratory diet	132	26 b
Clean control	129	74 c

Table 10, continued

	TEST B	
Swabbed with pheromone extract from females fed honeydew diet		
6 DE	48	40 a
12 DE	45	24 a
23 DE	67	22 a
Swabbed with pheromone extract from females fed laboratory diet		
6 DE	45	31 a
12 DE	60	38 a
23 DE	53	25 a
Clean control	88	97 b

In Test A, values followed by the same letter, and in Test B acceptance values of similar DE treatments of either diet followed by the same letter (e.g. 6 DE of extract from females fed honey dew diet vs. 6 DE of extract from females fed lab. diet), are not significantly different at the 5% level according to a G test

Evaluation of the effect of diet on ODP production was necessary because gut contents appear to comprise most of material released in ODP deposition (Prokopy et al. 1982c) and because of the debate on possible effects of diet and host substances on pheromone production (e.g. Hardee 1970, Hendry 1976, Miller et al. 1976, Byers 1983, Wiygul and Wright 1983.)

Fruit size

Offered a random series of small and large hawthorns, flies spent a significantly longer time marking large (22 secs) vs. small fruit (17 secs), but there were no statistically significant differences for either trail length (45.9 vs. 38.9 mm) or trail area (2.9 vs. 2.5 mm^2) (Table 11).

In Chapter IV, I showed that pheromone depositing females observed in the lab. and field dragged their ovipositors for a significantly longer time and distance on large 20 mm vs. small 12 mm diam hawthorns. The difference between time spent marking small vs. large fruit was more pronounced (ca. 40% greater) in the test series reported in Chapter IV than in the present study. This may be due to sampling error, although a large number of observations was made, or due to the fact that the size difference between offered fruit was slightly greater in

Table 11. Mean time spent during pheromone deposition (ovipositor extended and dragging on fruit surface), and mean length and area of oviposition-deterring pheromone substance (= trail) produced by 18 R. pomonella flies when dragging on large (18-19 mm diam) or small (12-13 mm diam) C. oxyacantha fruit. Values are means ± SD.

Fruit size	Time spent dragging (sec)	Trail length (mm)	Trail area (mm^2)
Small	17 ± 10 a	38.9 ± 25.3 a	2.5 ± 1.8 a
Large	22 ± 12 b	45.9 ± 29.8 a	2.9 ± 1.9 a

Values in the same column followed by the same letter are not significantly different at the 5% level according to a t-test

the Chapter IV test series. Alternatively, the difference might be due to apple origin flies being used in the present test series vs. hawthorn origin flies in Chapter IV. Recent work by Prokopy et al. (1982b) examining comparative behavioral traits suggests that there may be substantial R. pomonella host race differences. It is conceivable that selective pressure for "fine-tuned," flexible dragging behavior may be relaxed in populations developing in apple where the larval carrying capacity may exceed 15 or more per fruit (Prokopy 1972, Cameron and Morrison 1974) and the amount of pheromone deposited by a single female does not much influence subsequently arriving females (Prokopy 1972). In contrast, flexible dragging behavior may be adaptively advantageous for populations on hawthorn because 1) larvae developing in multiply infested fruit may realize lowered survivorship, 2) the amount of pheromone deposited following a single ovipositional bout is sufficient to deter most females from further egglaying, and 3) more pheromone is necessary to elicit female deterrence on large (20 mm diam) fruit vs. small (12 mm diam) fruit (Chapter IV).

Pheromone-marked and unmarked fruit

If amount of pheromone deposited were a flexible trait, then flies might deposit less pheromone on fruit

Table 12. Mean time spent during pheromone deposition (ovipositor extended and dragging on fruit surface), and mean length and area of oviposition-deterring pheromone substance (= trail) produced by *R. pomonella* flies (N = 20) when dragging on pheromone-marked* or clean *C. oxyacantha* fruit. Values are means ± SD.

Fruit treatment	Time spent dragging (sec)	Trail length (mm)	Trail area (mm^2)
Pheromone-marked	21 ± 14 a	30.6 ± 30.6 a	1.5 ± 1.4 a
Clean	33 ± 21 b	23.1 ± 18.3 a	1.3 ± 1.4 a

Values in the same column followed by the same letter are not significantly different at the 5% level according to a t-test

*Pheromone marked fruits were prepared by applying an aqueous solution of oviposition deterring pheromone

that were already pheromone-marked. Table 12 shows that females deposited essentially the same amount of trail substance per fruit when offered a random sequence of pheromone-marked or unmarked fruit (trail length = 30.6 vs. 23.1 mm and trail area = 1.5 vs. 1.3 mm , respectively). Although flies deposited similar quantity of trail substance on both fruit treatments, they spent significantly less time engaged in trail deposition behavior on pheromone marked vs. unmarked fruit (21 vs. 33 secs, respectively). Females became "nervous" or "skittish" when they contacted pheromone-marked fruit and, as a result, moved more quickly over the fruit surface while engaged in pre-oviposition behavior and dragging.

Summary

In conclusion, my results suggest that numerous factors may affect the quantity or quality of pheromone released not only by different R. pomonella females, but also from one dragging bout to the next by the same female. Of the several factors examined, changes in fly quality (i.e. fly age and size) and starvation produced the greatest differences in pheromone deposition while changes in fly experience, fly diet, or fruit

characteristics (size or presence of pheromone marking) produced less pronounced or no differences. Overall, these results lead one to suspect that variable pheromone deposition by R. pomonella females in nature may occur in response to a constellation of ecological conditions.

C H A P T E R I I I

RESIDUAL ACTIVITY OF OVIPOSITION-DETERRING PHEROMONE IN *RHAGOLETIS POMONELLA* AND FEMALE RESPONSE TO INFESTED FRUIT

Introduction

The stability of a resource partitioning system that relies on a chemical stimulus such as a pheromone to mediate against overcrowding may be influenced by a diversity of factors such as the production, release, reception, and residual properties of the stimulus involved. In regard to the latter, persistence of a pheromone may vary over time according to the species of insect and the nature of the message conveyed. For example, a repellent pheromone deposited by *Xylocopa* bees following extraction of nectar from passion flowers persists for only about 10 minutes, the time required for at least partial nectar replenishment (Frankie and Vinson 1977), whereas *Pieris brassicae* butterflies deposit an oviposition deterring pheromone during egg-laying which is deterrent for more than 14 days, the maximum time required for egg incubation (Schoonhoven *et al.* 1981).

Among other phytophagous insects that utilize oviposition-deterring pheromones to signal recognition of

previously infested plants or plant parts, deterrent components from occupied resources may be emitted until completion of larval development, such as pheromonal release by larvae of Ephestia, Plodia, and Heliothis (Prokopy et al. 1984). On the other hand, as far as is known, the oviposition-deterring pheromones produced by over a dozen different species of tephritid fruit flies are characterized by moderate residual activity and water solubility. As a result, several researchers have questioned the effectiveness of these pheromones as mediators of uniform egg dispersion and larval competition: pheromonal activity may break down prior to completion of larval development and, in climates with moderate to high precipitation, activity conceivably may be lost rather quickly (Katsoyannos 1975, Girolami et al. 1981, Prokopy et al. 1984). Here, one might suspect selection would favor female detection of larvae, or their effects.

Although studies aimed at understanding the ecological significance of these chemical stimuli are of interest to many researchers, most data concerning residual activity of ODP's have been generated by applied entomologists: if oviposition-deterring pheromones could be isolated, identified and synthesized, spraying host crops might become an important new approach to pest

management, especially if used in conjunction with appropriate traps to capture deterred females (Prokopy 1972, 1976; Katsoyannos and Boller 1976, 1980).

In the laboratory and field, I investigated the residual activity of R. pomonella pheromone over time under dry conditions as well as following exposure to varying intensities and durations of natural and simulated rainfall. Further, because it appeared that host discrimination mediated by pheromone broke down before completion of larval development, I determined whether females could discriminate against larval-infested fruit.

Materials and Methods

All flies bioassayed in lab. tests and utilized for fruit infestations or pheromone collections emerged from puparia formed by larvae that infested Crataegus hawthorns. Adults were maintained at 25°C, 60% RH and 16L:8D photoperiod in 30 x 30 x 30 cm Plexiglas-screen cages and provided a diet of sucrose, enzymatic yeast hydrolyzate and water.

Unless indicated, for all bioassays of female response to various fruit treatments, Downy hawthorns

(Crataegus mollis) were used. A total of 5-9 treated and control assay fruit were hung 6-8 cm apart from the ceiling of a Plexiglas-screen (30 x 30 x 30) observation cage. Unless otherwise stated, four cages were observed simultaneously and at least 20 different flies were bioassayed. A single mature R. pomonella female which had just begun oviposition in a clean fruit attached to the end of a dissecting probe was introduced into the assay cage by placing the probe near the cage floor. The female was allowed to fly to an assay fruit overhead and subsequently allowed to visit assay fruit for up to 2 hr. Females were excluded from tests if they rejected several (ca. 5) successive clean fruit. Acceptance (attempting oviposition before leaving) or rejection (leaving without attempting oviposition) was recorded for each visit to a fruit. When a female did accept a fruit, she was, immediately following egg deposition, gently transferred to a non-assay fruit, where she commenced and completed ovipositor dragging. In this way, no assay fruit were contaminated by pheromone deposited by assay females.

Oviposition-deterring pheromone residual activity over time under dry conditions

In June 1980, fresh picked, 15 mm diam sour cherries were placed in a high humidity plastic box, and either 14,

10, 7, 3, or 0 days prior to behavioral bioassays of pheromone activity. I used cherries in place of hawthorns because they were available and less likely to rot as rapidly. Each of several fruit was pheromone marked by five R. pomonella females. This level of pheromone deposition is known to be highly deterrent to arriving females. To obtain pheromone-marked fruit free of egg infestation, females that had just oviposited in a non-assay fruit were transferred to assay fruit, where they commenced and completed ovipositor dragging. Unmarked control fruit were held in an identical manner as treated fruit. All treatments were bioassayed simultaneously. Bioassays were run with five treated fruit (marked 14, 10, 7, 3, or 0 days prior to assay) plus 2 clean control fruit. The experiment was replicated twice.

A second series of sour cherries was maintained as above, but at 14, 10, 7, 3, or 0 days prior to bioassay, several fruit were swabbed with a water extract of oviposition deterring pheromone. Pheromone extract was prepared as follows: pheromone was collected by rinsing hawthorns used for oviposition with a known volume of distilled water. The amount of pheromone collected was estimated by counting the number of oviposition punctures in each washed fruit: 1 puncture = 1 dragging bout

equivalent (DE). In this experiment, I applied a concentration of 30 DE/fruit, an amount known to elicit a high level (ca. 89%) of fruit rejection by egglaying females. Bioassays were set up as in the above experiment, and the experiment was replicated twice.

Residual activity of pheromone in the field was evaluated in August 1980 using 18 or 19 mm diam unpicked C. mollis fruit. Five R. pomonella females were allowed to deposit pheromone on a single fruit either 21, 16, 12, 8, 4, or 0 days prior to bioassay (= treated). As with laboratory held fruit, marking females were not allowed to oviposit in the assay fruit. All pheromone-marked and clean control fruit were protected from rainfall by plastic hoods with mesh sides and bottom. Bioassays were run with 6 treated fruit plus 2 clean, control fruit.

Effect of rainfall on oviposition-deterring pheromone activity

In summer 1980 and 1983, 15-16 mm diam C. mollis fruit, which had been picked the previous season and refrigerated for up to 9 months, were pheromone marked in the lab. Females were allowed to deposit an amount of pheromone equivalent to 6 dragging circles/fruit (one dragging circle = ovipositor extended over a distance equivalent to the circumference of the fruit). Fruit were

pheromone marked 10 min to 2 hr prior to rainfall initiation, and along with clean control fruit, were hung by wires among natural growing clusters of C. mollis in the field. Several additional pheromone-marked fruit were similarly hung, but were rain-protected by plastic hoods as described above. Individual bioassays were run with 2 each of: rain exposed, clean control fruit; rain exposed pheromone-marked fruit; and pheromone-marked non-rain exposed fruit. Following each rain event, fruit were bioassayed using a minimum of 12 flies.

Effect of simulated rain on oviposition-deterring pheromone activity

Fruit were prepared as above for field tests, but were hung on wires and exposed to simulated rainfall. Artificial rain was produced using an adjustable sprinkler attached to a garden hose. Sixteen mm diam fruit marked with 6 dragging circles were bioassayed following two different intensities of artificial rain: light-moderate (4.5 mm/hr) and extremely heavy (32 mm/hr). Several of these fruit were collected following each of 0, 1/2, 1, or 2 hours of rain exposure. Control fruit (= unmarked) were exposed to the rainfall for 2 hours. Bioassays consisted of 4 pheromone marked fruit (exposed 0, 1/2, 1 or 2 hrs to rainfall) and 2 clean (rainfall-exposed) controls. Each

simulated rain type was replicated twice, on different days.

Effect of the presence of a developing larva on fruit acceptance by ovipositing females

Because a bacterial rot destroyed the unpicked infested C. mollis fruit used in 1981 and 1982, I ran the following tests using picked sour cherries and Crataegus oxyacantha hawthorns.

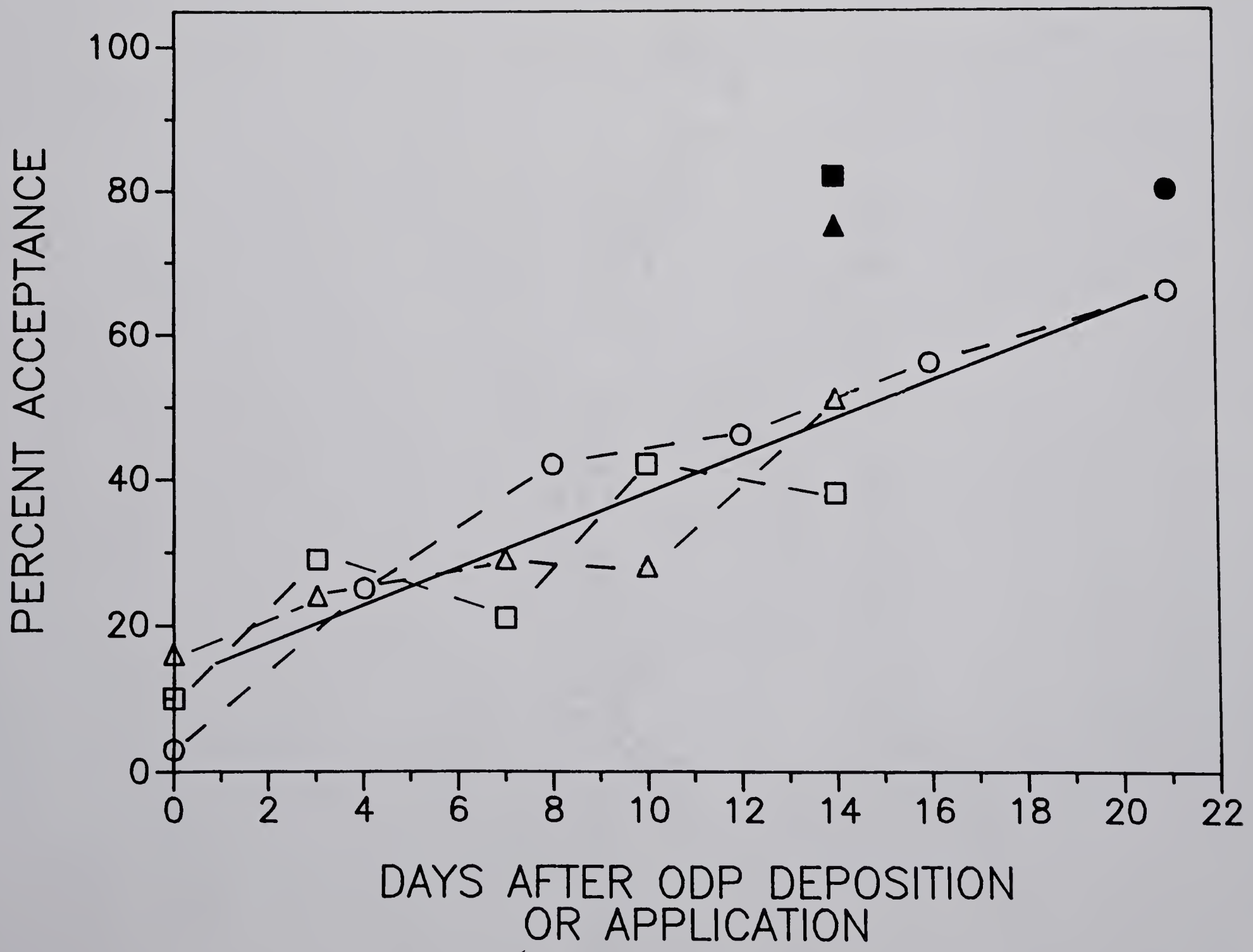
Freshly picked, 15 mm diam sour cherries were placed in a high humidity plastic box (= day 0). On days 0, 5, and 9, several fruit were infested by allowing a female to oviposit a single egg. Females were not allowed to deposit pheromone. Control fruit were held in an identical manner as infested fruit. Bioassay of infested fruit was run on day 14, so fruit possibly containing a single first, second, or third instar larva could be bioassayed simultaneously. The response of a total of 9 individual flies was observed in each of 3 bioassay cages containing 6 presumably infested fruit plus two control fruit. Upon completion of bioassays, dissection of fruit revealed that a total of 5 bioassay fruit contained no larvae, 5 contained a first instar, 4 a second instar, and 5 a third instar.

For C. oxyacantha tests, naturally infested, 9 mm diam fruit were picked on the day of bioassay. Fruit were inspected for oviposition punctures, thoroughly washed to remove ODP, and then 6 singly punctured fruit and 2 unpunctured fruit were included in a bioassay. Fifteen flies were observed in each of 4 bioassay cages. Dissection of fruit revealed that a total of 2 bioassay fruit contained no larvae, 4 contained a first instar, 6 a second instar, and 12 contained a third instar.

Results

Under dry conditions, a relatively linear decline in activity of R. pomonella ODP over time was observed both under lab and field conditions (Fig. 2). Analysis of covariance (Dunn and Clark 1974) to test for differences among the separate least squares lines of the 3 test conditions ($F_{2,12} = .29$, $p > .10$, ns) indicated that the combined data could be well described by a single regression line. Thus, there were no significant differences in rate of decline of activity under lab vs. field conditions or between female-deposited vs. extract applied ODP. Further, the pheromone proved moderately stable, even on growing fruit under natural conditions, with some activity persisting after 3 weeks. For the

Figure 2. The residual activity over time of R. pomonella ODP under dry conditions in the lab. or field. Treatments were: fly-marked fruit that were held in the lab (□) and the corresponding clean control fruit (■); field-exposed, fly-marked fruit (○) and control fruit (●); ODP extract marked fruit that were held in the lab (△) and control fruit (▲). "Fly-marked" fruit were pheromone-marked by 5 R. pomonella females. All treatments within a test were bioassayed simultaneously; thus, values for control fruit are represented by a single point. The least squares regression line for all data points (solid line) is shown ($y = 12.6 + 2.5\ x$; $r^2 = .86$, $N = 16$).


PERCENT ACCEPTANCE
100
80
60
40
20
0
0
2
4
6
8
10
12
14
16
18
20
22
DAYS AFTER ODP DEPOSITION
OR APPLICATION

combined data, the half-life of ODP was 10.7 days. This was calculated from the regression equation of days after ODP deposition or application on log (percent rejection of fruit treatments): $y = 4.29 - 0.0645\ x$. Because overall rejection of unmarked control fruit was approximately 20%, the line was shifted by subtracting 20% from each % rejection value to account for this "background".

A distinct decline in pheromone activity resulted from exposure to both natural and simulated rainfall (Figs. 3 and 4). For each storm, percent loss in pheromone activity was established by: 1) calculating the difference between percent acceptance of clean control fruit and pheromone-marked, non-rain-exposed fruit, 2) calculating the difference between pheromone-marked, rain-exposed fruit and pheromone-marked non-rain-exposed fruit and 3) determining percent loss by calculating what percentage the second value is of the first. In nature, the most severe impact on pheromone persistence followed a torrential 20 min downpour and a heavy 4 1/2 h rain where 61% and 50%, respectively, of activity was lost. Substantially less activity (ca. 13%) was lost following exposure to a 20 min shower, whereas an intermediate loss (21-35%) in activity resulted from two longer-term (12 and 23 h) light rains and a 7.3 h moderate rain (Fig. 3). Tests of simulated rainfall (Fig. 4) produced similar

Figure 3. The residual activity of R. pomonella ODP exposed to various durations and intensities of natural rainfall. Treatments were: clean control, rain-exposed fruit (▭); ODP-marked, non-rain-exposed fruit (▨); ODP-marked, rain-exposed fruit (▨). Values above bars represent the number of female arrivals on each fruit treatment.

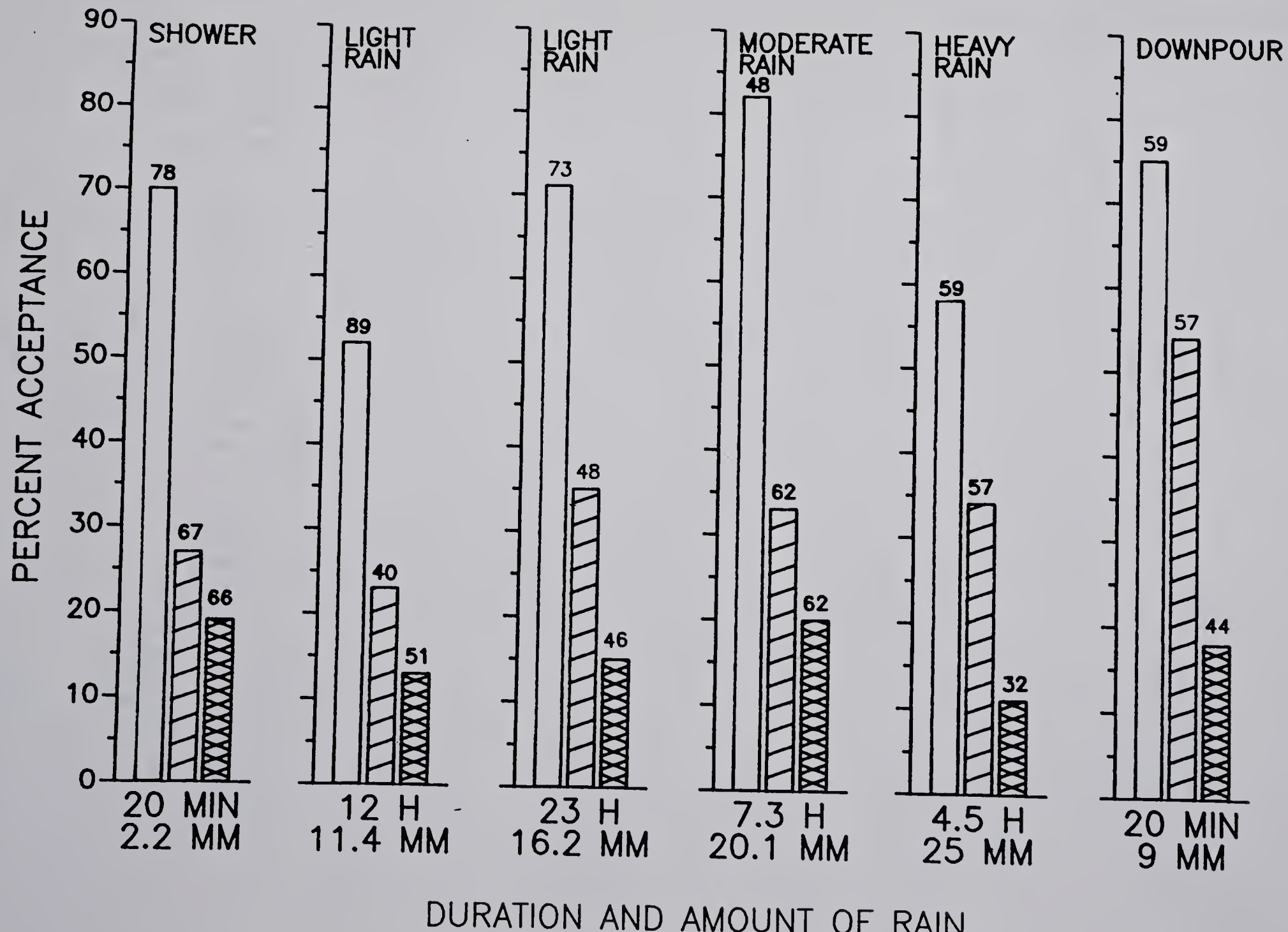
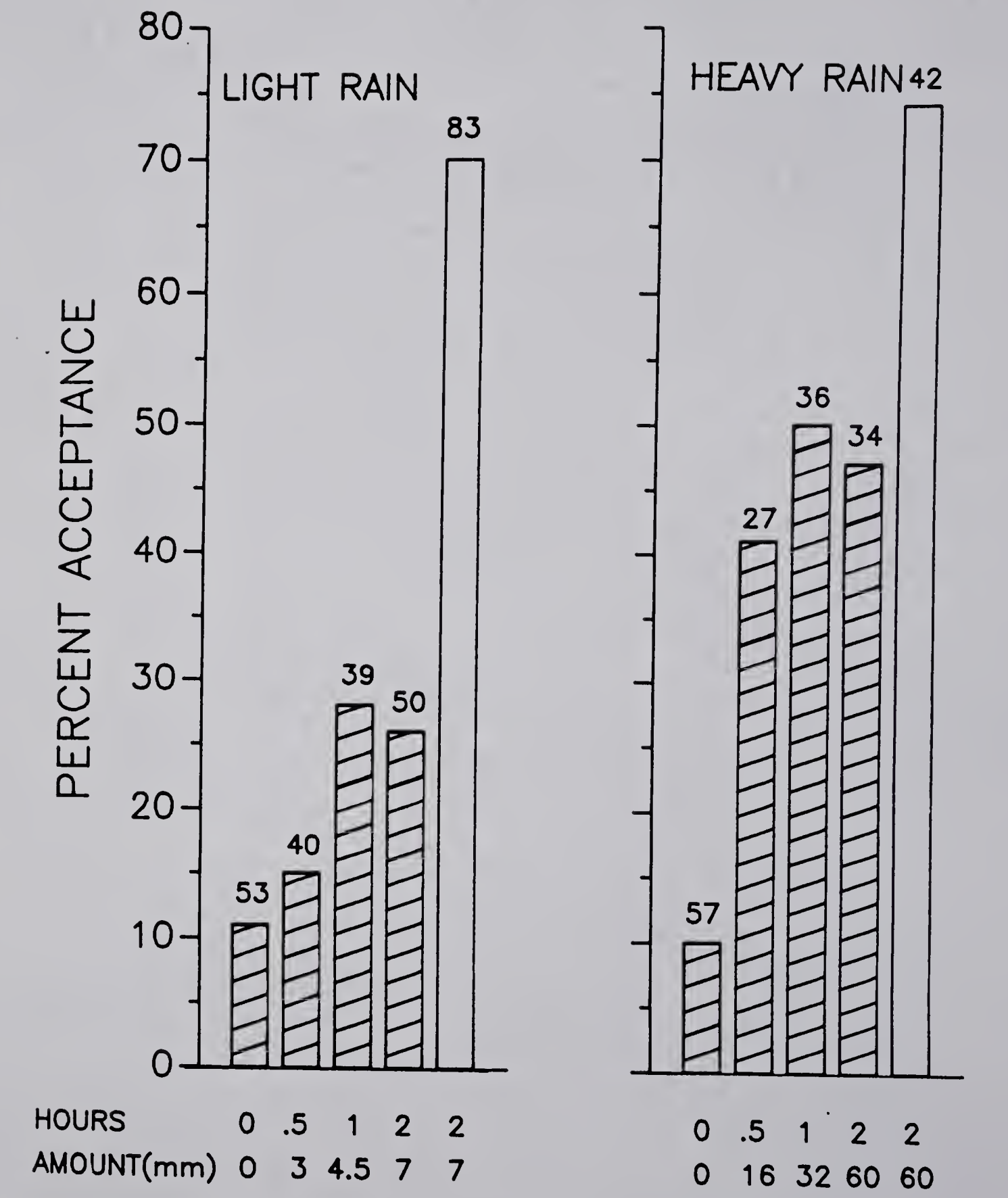

PERCENT ACCEPTANCE
90
80
70
60
50
40
30
20
10
0
SHOWER
78
67
66
20 MIN
2.2 MM
LIGHT RAIN
89
40
51
12 H
11.4 MM
LIGHT RAIN
73
48
46
23 H
16.2 MM
MODERATE RAIN
48
62
62
7.3 H
20.1 MM
HEAVY RAIN
59
57
32
4.5 H
25 MM
DOWNPOUR
59
57
44
20 MIN
9 MM
DURATION AND AMOUNT OF RAIN

Figure 4. The residual activity of R. pomonella ODP exposed to various durations of a light or heavy simulated rainfall. Treatments were ODP-marked, rain-exposed fruit (▨); clean control, rain-exposed fruit (□). Values above bars represent the number of female arrivals on each fruit treatment.



DURATION AND AMOUNT OF ARTIFICIAL RAIN

losses in ODP activity: following 1/2, 1 or 2 hr exposures to a light-moderate rain, approximately 8, 34 and 30% total activity, respectively, was lost. Following 1/2, 1 or 2 hr exposures to a very heavy simulated rainfall, approximately 62, 76, and 70% total activity, respectively, was lost.

Females were able to discriminate against fruit containing second or third conspecific larvae (Table 13). Fewer ($p < .05$, G test) females attempted oviposition in cherries (Test A) that contained a third instar larva (31% acceptance) than in controls (70%) or fruit containing a first (63%) or second instar larva (52%). Discrimination against infested fruit was stronger in the smaller C. oxyacantha hawthorns (Test B). Acceptance of fruit containing a second instar larvae (33%) was less ($p < .05$, G test) than that of controls (56%) or fruit containing a first instar larva (53%), and only 2% of females tested accepted fruit containing a third instar larva.

Discussion

Stability over time of R. pomonella oviposition deterring pheromone demonstrated here confirms and expands

Table 13. Female R. pomonella acceptance of 15 mm diam sour cherries (Test A) or 9 mm diam C. oxyacantha hawthorns (Test B) infested with one conspecific larva

TEST A

Treatment	Number of female arrivals on fruit	% boring attempts
clean control	33	70 a
1st instar	32	63 a
2nd instar	31	52 ab
3rd instar	32	31 b

TEST B

Treatment	Number of female arrivals on fruit	% boring attempts
clean control	50	56 a
1st instar	15	53 a
2nd instar	40	33 b
3rd instar	106	2 c

Values in the same column followed by the same letter are not significantly different at the 5% level according to a G test

on earlier work under under dry laboratory conditions with this and other tephritids. This includes a previous study on R. pomonella showing high pheromone persistence for at least 4 days under dry conditions (Prokopy 1972), as well as studies of western cherry fruit fly, Rhagoletis indifferens (Mumtaz and Aliniazee 1983), Caribbean fruit fly, Anastrepha suspensa (Prokopy et al. 1977), Mediterranean fruit fly, Ceratitis capitata (Prokopy et al. 1978), black cherry fruit fly, Rhagoletis fausta (Prokopy 1975), and European cherry fruit fly, Rhagoletis cerasi (Katsoyannos 1975), showing substantial persistence under dry conditions for 4, 6, 6, 9, and 12 days, respectively. Perhaps the active components of these moderately stable oviposition-deterring pheromones of tephritids are similar in chemical identity.

Other insects respond to oviposition deterrents (of either insect or plant origin) that persist for days or weeks. Persistent pheromones include those of the sorghum shootfly, Atherigona soccata (Raina 1981), Pieris brassicae butterflies (Schoonhoven et al. 1981), Trichoplusia ni (Renwick and Radke 1980, 1982), the European corn borer, Ostrinia nubilalis (Dittrick et al. 1983), and the endoparasitoid, Telenomus fariai (Bosque and Rabinovich 1979).

Data presented here and in other studies (Prokopy

1972, Prokopy et al. 1982c) demonstrate that R. pomonella ODP is highly soluble in water. Indeed, most known oviposition deterrents are water soluble, including those of such tephritids as Rhagoletis indifferens (Prokopy et al. 1976, Mumtaz and Aliniazee 1983), the South American fruit fly, R. fraterculus (Prokopy et al. 1982a), R. fausta (Prokopy 1975), R. cerasi (Katsoyannos 1975), A. suspensa (Prokopy et al. 1977), C. capitata (Prokopy et al. 1978), eastern cherry fruit fly, (R. cingulata), the blueberry maggot fly (R. mendax), two species of dogwood berry flies (R. cornivora and R. tabelaria) (Prokopy et al. 1976), the rose hip fly (R. basiola) (Averill and Prokopy 1981), and the snowberry fly (R. zephyria) (Averill and Prokopy 1982), as well as the parasitoids Telenomus sphingis (Rabb and Bradley 1969) and T. fariai (Bosque and Rabinovich 1979), the alfalfa blotch leafminer (Agromyza frontella) (McNeil and Quiring 1983), the sorghum shootfly (Raina 1981), the European corn borer (Dittrick et al. 1983) and Pieris brassicae butterflies (Schoonhoven et al. 1981).

The water solubility of R. pomonella ODP may lessen its efficacy in field applications. Indeed, Katsoyannos and Boller (1980) found a reduced effect of Rhagoletis cerasi ODP sprays on cherry trees following a heavy rainfall. In my simulated rain tests, some pheromone

activity remained, even following a 2 hour heavy washing. Perhaps some ODP compounds bind to fruit surface components, or perhaps feces slow the release of ODP. This possibility, combined with partial protection of ODP marked fruit afforded by foliage cover, may result in at least some retention of pheromone effectiveness even under substantial rainfall conditions.

Although R. pomonella ODP seems a poor resource partitioning cue because of its water solubility and only moderate stability, its disadvantages may be balanced by such considerations as low physiological costs of producing and maintaining such an ODP system (Prokopy 1981; Roitberg, personal communication). Alternatively, ODP deposition and recognition may originally have served to deter a female from hawthorn fruit already containing one of her own eggs. In such a case, the pheromone may need be only short-lived, owing to the fact that a foraging female tends to lay a single egg per fruit until all clean fruit are exhausted in a cluster (personal observation). She then usually moves to the adjacent cluster until she has laid about 10 or so eggs per day. In the evening, the female often moves to and remains in the tree top (Prokopy et al. 1972), and, as there usually are thousands of hawthorn fruit per host tree, it would be unlikely that she would revisit the same clusters the

following day.

Further, the pheromone may need deter egglaying only until other partitioning factors come into play: R. pomonella larval infestation promotes premature abcission, and females are able to detect developing larvae or their effects. With small fruit, where larval competiton is exceptionally intense (Chapter IV), I found that females clearly are able to discriminate against fruit within 8-10 days following introduction of an egg. In larger (15 mm diam) fruit, significant discrimination occurs against fruit 12-14 days following infestation (when third instars were present), although reduced acceptibility occurred after 8-10 days.

The tephritids, R. fausta and A. suspensa, which also lay a single egg per fruit, were not influenced by presence of first or second instar larvae in 15 mm diam host fruit (Prokopy 1975, Prokopy et al. 1977), but response to presence of third instar larvae or to larvae developing in smaller fruit was not evaluated. Among tephritids which lay a clutch of eggs per ovipositional bout, R. completa, C. capitata, Dacus cucurbitae, and D. tyroni all discriminate against fruit infested with early instar larvae (Cirio 1972, Fitt 1984, Prokopy and Koyama 1982). As in R. pomonella, Fitt (1984) found that D. tyroni females more strongly discriminate against small

fruit containing larvae. He suggested that in such fruit, larvae are relatively closer to the fruit surface than would be the case in a larger fruit. Thus, larval activity (movement) or effects (e.g. release of volatile deterrents of larval or fruit origin from lacerated tissue) would be more easily detected by ovipositing females.

I did not study how R. pomonella females discriminate against larval infested fruit. Discrimination occurred after landing, because similar numbers of females visited infested and uninfested fruit. Further, neural receptors on the ovipositor apparently are not involved because females were able to discriminate against infested fruit without probing. Females that did insert the ovipositor were just as likely to complete egglaying in infested fruit as in uninfested fruit. These results suggest that females utilize short range olfactory receptors, contact chemoreceptors or mechanoreceptors to discriminate against fruit containing larvae. In studies of other tephritids, Girolami et al. (1981) reported that volatile deterrents released from olive tissues attacked by Dacus oleae elicit female deterrence and Fitt (1984) showed that oviposition was inhibited by decomposed host tissue from which larvae had been removed. Fitt (1984) notes that chemical changes in the host may be due to

proliferation of bacteria which release an inhibitory chemical. Bacteria are thought to be important or essential for larval development of several tephritid species, including R. pomonella (Allen and Riker 1932, Allen et al. 1934; Prokopy 1977, but see Howard et al. 1985). Further, the possibility that female R. pomonella are able detect larval movements within the fruit cannot be ruled out. Two parasitic wasps, Biosteres longicaudatus and Opius oelleus, utilize host vibration cues to locate their larval hosts (Lawrence 1981; Glas, personal communication).

C H A P T E R I V

PHEROMONAL MEDIATION OF COMPETITION IN *RHAGOLETIS POMONELLA*

Introduction

The involvement of chemical or visual oviposition deterrents in signalling recognition of previously or currently utilized resource sites has been demonstrated in a growing number of insect species (Prokopy *et al*. 1984). High mortality and other adverse effects of intraspecific competition that result from overload of resource sites presumably act to confer a selective advantage on females that respond to oviposition-deterring signals and seek more suitable egg-laying sites elsewhere.

In this chapter, I report studies of intraspecific larval competition in *Rhagoletis pomonella* and evaluate the role of oviposition-deterring stimuli in mediating such competition. Specifically, I sought to establish the presence and severity of larval competition occurring in natural populations of the apple maggot in Downy hawthorns (*Crataegus mollis*), a native host species of this insect. I studied the potential role of oviposition-deterring stimuli by evaluating the following hypotheses: 1) the

amount of fruit surface area phermonally marked by a female following egglaying is related to the amount of food or space requirements of a developing larva, and 2) because the oviposition deterring pheromone is both water soluble and only moderately stable (Chapter III), pheromone need deter oviposition only long enough to give the earliest developing larva a headstart, and thus, a competitive advantage over later developing larvae.

Materials and Methods

Larval Competition

Crataegus mollis hawthorn fruit were collected from field sites and the number of oviposition punctures in each was recorded. Three sizes of the roughly spherical fruit (small: diam = 12 mm, surface area = 1,810 mm^2, volume = 7,236 mm^3; medium: diam = 15 mm, surface area = 2,827 mm^2, volume = 14,113 mm^3; large: diam = 20 mm, surface area = 5,027 mm^2, volume = 33,510 mm^3) were selected for collection, spanning the range of naturally occurring sizes. The surface area of medium and large fruit was 1.6 and 2.8 times greater, respectively, than small fruit whereas the volume of medium and large fruit

was approximately 1.9 and 4.6 times greater, respectively, than small fruit. Care was taken such that no fruit with existing larval emergence holes were collected. Larvae began to emerge from fruit within 1 day following collection. Dissection of additional fruit collected at the same time as the above indicated that for 94% of fruit examined, an oviposition puncture indicated the presence of an egg. Thus, puncture number and egg density will be terms used interchangeably in this study.

Collected fruit were held individually and emerging larvae counted daily. Note was taken of multiply emerging larvae from the same fruit. Following puparial formation, individuals were weighed ($\bar{x} \pm SE$). The term pupal weight is used to designate the weight of the prepupa plus its puparium. Survivorship data is presented as percent of total eggs per fruit that survived to puparial formation for each initial density.

Pupae that developed under varying larval densities in medium-sized fruit were placed in diapause conditions for 7 months. Following this, all such pupae were incubated at 26^{O}C, 65% RH, and 16L:8D until adults emerged. Adults were maintained individually in small plastic-screen cages and fed a diet of sucrose, enzymatic yeast hydrolyzate and water. A single clean C. mollis fruit was introduced daily to each female and the number

of eggs deposited per fruit was counted the following day. Number of days to female reproductive maturity, lifetime fecundity of females, and female and male longevity were recorded.

Oviposition-deterring pheromone as a mediator of larval competition

First, to evaluate the hypothesis that the amount of fruit surface marked by a female following oviposition correlates with the amount of food or space required by a larva to grow to maturity, it was necessary to determine the average amount of pheromone deposited by a female following a single egglaying. This amount is designated as equivalent to one dragging bout. Pheromone-depositing females were observed both in the lab and field as they marked small, medium, and large C. mollis fruit. Duration of pheromone trail deposition was timed and the number of times a fly dragged a distance that approximated the circumference of the fruit (= one dragging circle) was estimated by eye. Dragging trail distance was calculated by multiplying estimates of dragging circle number by fruit circumference. I assumed that length of pheromone trail to be equivalent to amount of pheromone deposited.

After the average number of dragging circles made by females during dragging bouts was established for each

fruit size, fruit with differing dragging bout numbers were bioassayed in the field and the lab. All R. pomonella assay adults originated from field collected pupae formed by larvae which infested C. mollis fruit. Adults were maintained in 25 x 25 x 25 cm plexiglas-screen cages and provided a diet as described above. For field bioassays, females were allowed to mark small, medium, or large fruit during 0, 1, 2, or 3 dragging bouts. Such fruit were attached to wires, and for a given assay, clusters of 5 same-size fruit (3 having 1, 2, or 3 dragging bout equivalents of pheromone and 2 being clean (no pheromone)) were assembled. Within a cluster, fruit were 2-5 mm apart. When mature, assay flies were transported to the study site, where tests were conducted on individual dwarf apple trees enclosed within 3.5 x 3.5 x 2.5 m nylon screen cages. Four clusters of same-sized, prepared fruit were hung approximately 15 cm apart on a branch 1-3 m above ground. Just before testing, each assay female was presented a clean, uninfested C. mollis fruit attached to the end of a dissecting probe. Those that completed egglaying and pheromone deposition and flew from the probe to the tree were allowed to forage among fruit clusters for up to 2 hr, or until they flew to the cage wall. The number of visits resulting in acceptance (attempted oviposition) and rejection (departure without

attempting oviposition) was recorded for each fruit treatment. During an assay, fruit could not be removed without disturbing the foraging female. Therefore, visits by an assay female to fruit that she had previously accepted for oviposition and subsequently marked with pheromone were recorded, but not included in final data analysis.

In lab bioassays, only medium-size C. mollis fruit were tested. Five treated (1 each marked with 1, 2, 3, 4, or 5 dragging bout equivalents) and 2 control fruit were hung 6-8 cm apart from the ceiling of a plexiglas-screen (30 x 30 x 30 cm) observation cage. From this point, bioassay procedures were identical to those described in Chapter II.

To evaluate possible competitive advantage afforded a larva given a headstart, females were radiolabeled by injection of 600,000 CPM of ^{32}P into the thorax. In this way, when both a labeled and unlabeled larva were present in the same fruit as a result of oviposition by a labeled and unlabeled female, reliable identification of the "winner" could be established. Preliminary studies demonstrated that a single-developing unlabeled larva had < 20 CPM at pupation while a labeled larva consistently had > 100 CPM. In this experiment, an insufficient supply of growing C. mollis forced use of unpicked, uninfested fruit

of the English hawthorn, Crataegus oxyacantha, an introduced ornamental host of R. pomonella. These fruit were more ellipsoid and substantially smaller (average = 9 cm diam and 12 cm long, volume = 4071 mm^3) than C. mollis fruit.

Flies were transported to the study site, their wings cut off, and were manipulated so as to accomplish the following treatments:

(1) either an unlabeled egg only or a labeled egg only was introduced into a fruit,

(2) fruit were doubly infested according to one of 3 patterns:

(i) both an unlabeled and labeled egg were introduced within 1 hr of each other (= same day),

(ii) an unlabeled egg was introduced, and 2 days later, a labeled egg was introduced,

(iii) the order of egg introduction was reversed, with the labeled egg receiving a 2-day headstart.

Natural fly infestation was prevented by caging treated fruit in fine mesh polyester screening. When the first larval emergence hole was noted, the fruit were picked and held individually. Larval development time in C. oxyacantha (average = 27 days) was longer than larval development time in C. mollis (average = 16 days). Each resulting pupa was weighed and then analyzed for 32P

content.

For comparison of means, Student-Newman-Keul's procedure (5% level of significance) was used.

Results and Discussion

Larval Competition

Survivorship. Mortality was high in multiply-infested hawthorn fruit (Fig. 5): regardless of fruit size, percent larval survivorship declined from over 70% in fruit containing a single egg to ca. 45-50% in fruit containing 2 eggs. For the three fruit sizes, the following exponential equations were fit following log tranformation of the dependent variable: small fruit: $y = 4.48 - 0.331 x$, $r^2 = .99$, $N= 7$; medium fruit: $y = 4.57 - 0.340x$, $r^2 = .97$, $N = 7$; large fruit: $y = 4.38 - 0.240x$, $r^2 = .93$, $N = 7$. Analysis of covariance (Dunn and Clark 1974) to test for differences among the three lines ($F_{2,11} = 5.58$, $p < .05$) indicated a significant effect of fruit size. Inspection of the data in Fig. 5 reveals that larval survivorship appears similar in small and medium fruit, but there was a trend toward enhanced survivorship in large fruit as density increased. This may be accounted for by the fact that in multiply-infested small fruit, only 1 or 2 larvae (never 3) survived to puparial

Figure 5. Effect of initial R. pomonella egg density on larval survivorship to puparial formation in C. mollis fruit.

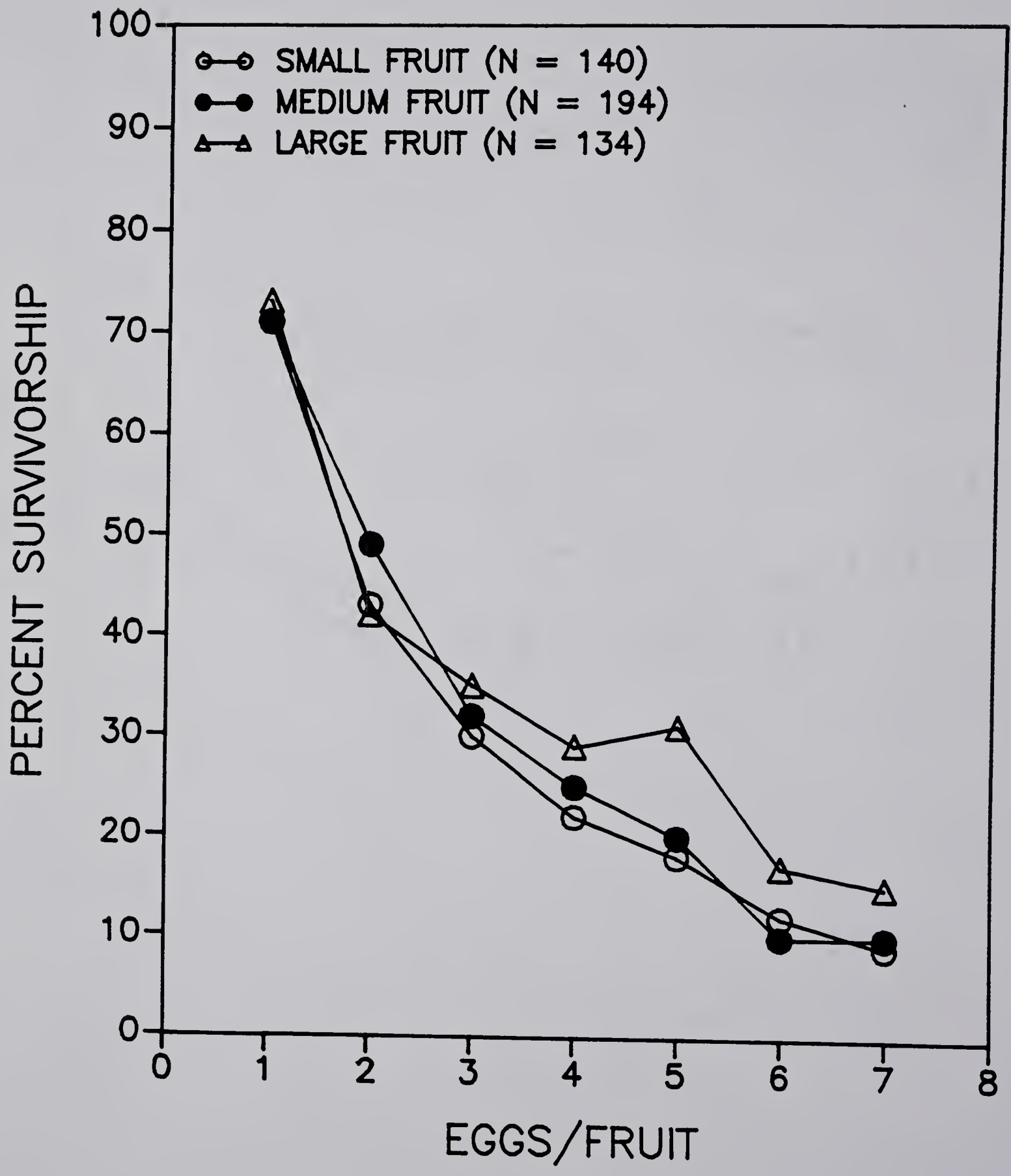
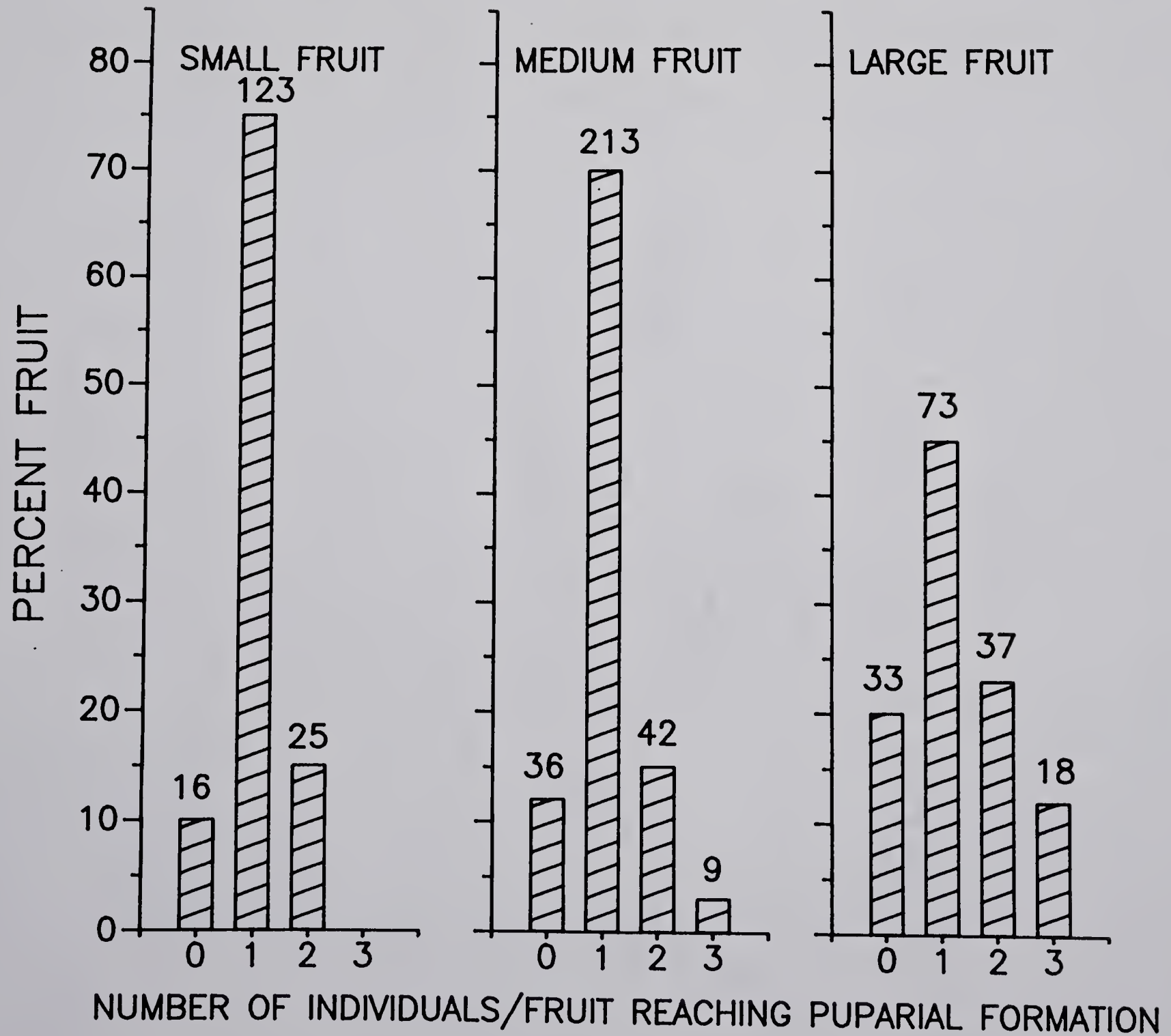

SMALL FRUIT (N = 140)
MEDIUM FRUIT (N = 194)
LARGE FRUIT (N = 134)
PERCENT SURVIVORSHIP
100
90
80
70
60
50
40
30
20
10
0
0
1
2
3
4
5
6
7
8
EGGS/FRUIT

Figure 6. Percentage of field collected C. mollis hawthorn fruit supporting 0, 1, 2, or 3 R. pomonella larvae to puparial formation. Values above bars represent N for each fruit category.


SMALL FRUIT
MEDIUM FRUIT
LARGE FRUIT
123
213
73
16
25
36
42
9
33
37
18
0
10
20
30
40
50
60
70
80
0 1 2 3
PERCENT FRUIT
NUMBER OF INDIVIDUALS/FRUIT REACHING PUPARIAL FORMATION

formation, while a third larva completed development in 3 and 12% of observed medium and large fruit, respectively (Fig. 6).

For R. pomonella in apple, Cameron and Morrison (1977) demonstrated a significant positive correlation between larval density and larval mortality . In a medium size apple, ca. 30% larval mortality occurred at low egg densities (10-15 larvae/fruit) as compared to ca. 90% mortality at higher egg densities (70 larvae/fruit). This range in densities reflected those in the field.

Positive correlation between larval density and larval mortality has been shown for numerous other insect species (see refs. in Peters and Barbosa 1977, Beaver 1967, Readshaw and van Gerwen 1983). In fact, Klomp (1964) noted that such a relationship has been found in nearly all investigations on intraspecific competition.

I found that although medium fruit had 2 times the volume of small ones (and presumably 2 times more larval resources), there was no significant difference in total survivorship of singly- or multiply-developing larvae. In fact, even in very small C. oxyacantha fruit (9 mm diam), which I found never to support development of more than a single dwarf individual and which apparently possess 1/8th the amount of resource of large C. mollis fruit (20 mm diam), larval survivorship was identical to that in large

C. mollis fruit, both for single infestations (70-75%) and double infestations (45%).

Unlike R. pomonella in hawthorn fruit, in the bean weevil, Callosobruchus maculatus, there was a positive correlation between survivorship of a single egg and bean weight, even in situations where all beans appeared to have ample resources to support one larva (Mitchell 1975).

Additionally, I found a significant correlation between initial egg density in 15 mm diam C. mollis and percentage of resulting pupae surviving to adults ($y = 87 - 5.86x$, $r^2 = .81$, $N = 7$). Data presented in Table 14 indicate that pupae originating from these medium-size hawthorns with initial egg densities of 1-4 eggs/fruit showed significantly higher survival (67-80%) to the adult stage as compared to survival of those originating from hawthorns with initial densities of 5-7 eggs/fruit (45-53%). In contrast, for R. pomonella developing in apple, pupal mortality was higher for individuals developing under lower densities as compared to higher densities (Cameron and Morrison 1977), possibly owing to severe competition removing a high proportion of the "less capable" larvae. Why this would occur in apple and not hawthorn is not easily explainable. An alternative explanation for Cameron and Morrison's results could be

Table 14. Relationship between initial R. pomonella egg density in 15 mm diam C. mollis fruit and percentage of resulting pupae surviving to adults.

Initial egg density	Number of pupae	Percentage of pupae surviving to adults
1	29	75 a
2	48	80 a
3	33	67 a
4	14	75 a
5	47	53 b
6	20	50 b
7	20	45 b

Values in the same column followed by the same letter are not significantly different at the 5% level according to a G test

that breakdown of the apple flesh, and thus larval accessibility to superior and abundant food resources, is enhanced under higher larval densities. Or, along this same line, recent findings of Courtice and Drew (1983) and Drew et al. (1983) suggest that tephritid larvae may be "grazers" on micro-organisms, which are transferred by adults to eggs and host tissue (but see Howard et al. 1985). If this were the case, larval development would depend less on total fruit flesh available than on total microorganism infected fruit. Possibly then, in contrast to hawthorn, in apple an "intermediate" larval density may be optimal: some degree of larval aggregation may be favored for maximum exploitation of fruit resources, but short of overcrowding. This may be a fairly widespread phenomenon in insects (Prokopy 1981).

Effect of initial egg density on pupal weight. The effect of initial egg density on mean pupal weight is presented in Table 15. Regression analysis of this data indicates a significant correlation between initial egg density and pupal weight for each of the fruit sizes (small fruit: $y = 10.8 - 0.79x$, $r^2 = .82$, $N = 125$; medium fruit: $y = 9.6 - 0.39x$, $r^2 = .91$, $N = 147$; large fruit: $y = 9.74 - 0.32x$, $r^2 = .87$, $N = 98$). Analysis of covariance to test for differences among the separate least squares

Table 15. Mean R. pomonella pupal weight in relation to initial egg density in C. mollis fruit.

Initial egg density	Mean pupal weight ± SE (mg)					
	N	small fruit	N	medium fruit	N	large fruit
1	35	10.60 ±.28 a	27	9.45 ±.31 a	15	9.53 ±.40 a
2	42	8.45 ±.38 b	44	8.82 ±.41 ab	22	8.84 ±.41 a
3	19	8.80 ±.53 b	33	8.12 ±.57 ab	27	9.08 ±.48 a
4	16	7.13 ±.37 b	14	7.85 ±.64 ab	19	8.22 ±.37 a
5	12	7.30 ±.40 b	37	7.92 ±.41 ab	12	8.31 ±.69 a
6	--	----	20	7.25 ±.54 b	10	7.81 ±.52 a

Means in the same column followed by the same letter are not significantly different at the 5% level

lines indicated a significant effect of fruit size ($F = 4.09$, $p < .05$). A pronounced effect was noted in individuals originating from small fruit. From the regression equations, we can see that the slope of decline in pupal weight was ca. 2x greater for small fruit vs. medium or large. Further, a significant decrease in mean pupal weight occurred if more than one larva developed in a small fruit (Table 15). Effects on pupal weight were much less pronounced among individuals originating from medium size or large fruit. For these, there was no significant difference in mean weight among individuals developing at any of the observed densities in large fruit, while in medium-size fruit, a significant decline in mean weight was observed only at the highest density examined, 6 eggs/fruit (Table 15). Nonetheless, for all fruit sizes, there was a significant trend toward decreasing mean pupal weight with increasing initial egg density. An increase in population density per unit of resource frequently is reflected in declining weight or size of resultant individuals has been documented for many other insects (Peters and Barbosa 1977).

The heaviest mean pupal weight was achieved by individuals developing singly in small fruit ($F = 3.47$, $p < .05$) (Table 15). Perhaps, if it turns out that R. pomonella larvae are in fact "grazers" on micro-organisms

in the host fruit (as discussed above), frequency of encounters with infected fruit flesh may be enhanced in smaller fruit.

Carrying capacity of fruit. While, as noted earlier, most C. mollis fruit produced a single larva, a second larva emerged from some small fruit, and a third larva from some medium and large fruit. Mean weights of these multiple emergers are presented in Table 16. There was no significant difference in pupal weights between first and second emergers from small, medium or large fruit, although for small fruit, the second larva was appproximately 1 mg (12%) lighter. In cases where larvae emerged as triplets from large and medium size fruit, large fruit supported the development of 3 similar-weight individuals, whereas the third emerger from medium fruit was substantially smaller (by 3.3 mg or 37%) than the first emerger. Thus, if we define a fruit's carrying capacity as the number of larvae that can develop without reduction in adult fitness, the carrying capacity of small C. mollis fruit is 2 larvae, of medium fruit is between 2-3 larvae, and of large fruit is unknown, but probably greater than 3 larvae. (See evidence presented in the next section relating pupal weights to adult fitness). If we define carrying capacity as the number of larvae that

Table 16. Mean R. pomonella pupal weights of successively emerging individuals from the same C. mollis fruit

	Mean pupal weight ± SE (mg)		
fruit size (N)	1st emerger	2nd emerger	3rd emerger
small (23)	8.93 ±.33 a	7.93 ±.81 a	-------
medium (19)	8.89 ±.55 a	8.16 ±.60 a	5.62 ±.62 b
large (24)	9.08 ±.64 a	8.89 ±.58 a	8.61 ±.67 a

Values in the same row or column are not significantly different at the 5% level

can develop in a fruit without reduction in larval survival, the carrying capacity is a single individual for each fruit size (Fig. 5).

Adult fitness. There was a significant correlation ($r = .92$, $p < .001$) between pupal weight and number of days to female maturity (= first egglaying) as well as between pupal weight and rate of oviposition (= number of eggs laid/day) ($r = .67$, $p < .001$) (Fig. 7 and 8). Females originating from the smallest pupae required 2-3 times longer (over 20 days in some cases) to lay their first egg. Further, these same females laid eggs less frequently, producing a lifetime average of only 2-5 eggs/day as compared to adults originating from larger pupae, whose mean daily lifetime fecundity exceeded 8 eggs. On the other hand, pupal size was was not significantly correlated with cumulative lifetime egg production, probably because there was a weak negative correlation ($r = -.33$, $p < .1$) between female longevity and pupal weight. Thus, over time, some long-lived, small females could in theory produce as many eggs as larger females, although they may require a significantly longer prereproductive period and lay significantly fewer eggs/day. Finally, pupal weight was not correlated with male longevity ($r = .13$) or time to eclosion of adults (r

Figure 7. Effect of R. pomonella pupal weight on number of days to first oviposition. The quadatric equation using polynomial least squares regression is $y = 68.4 - 12.0x + 0.610x^2$, $r^2 = .85$, N = 25.

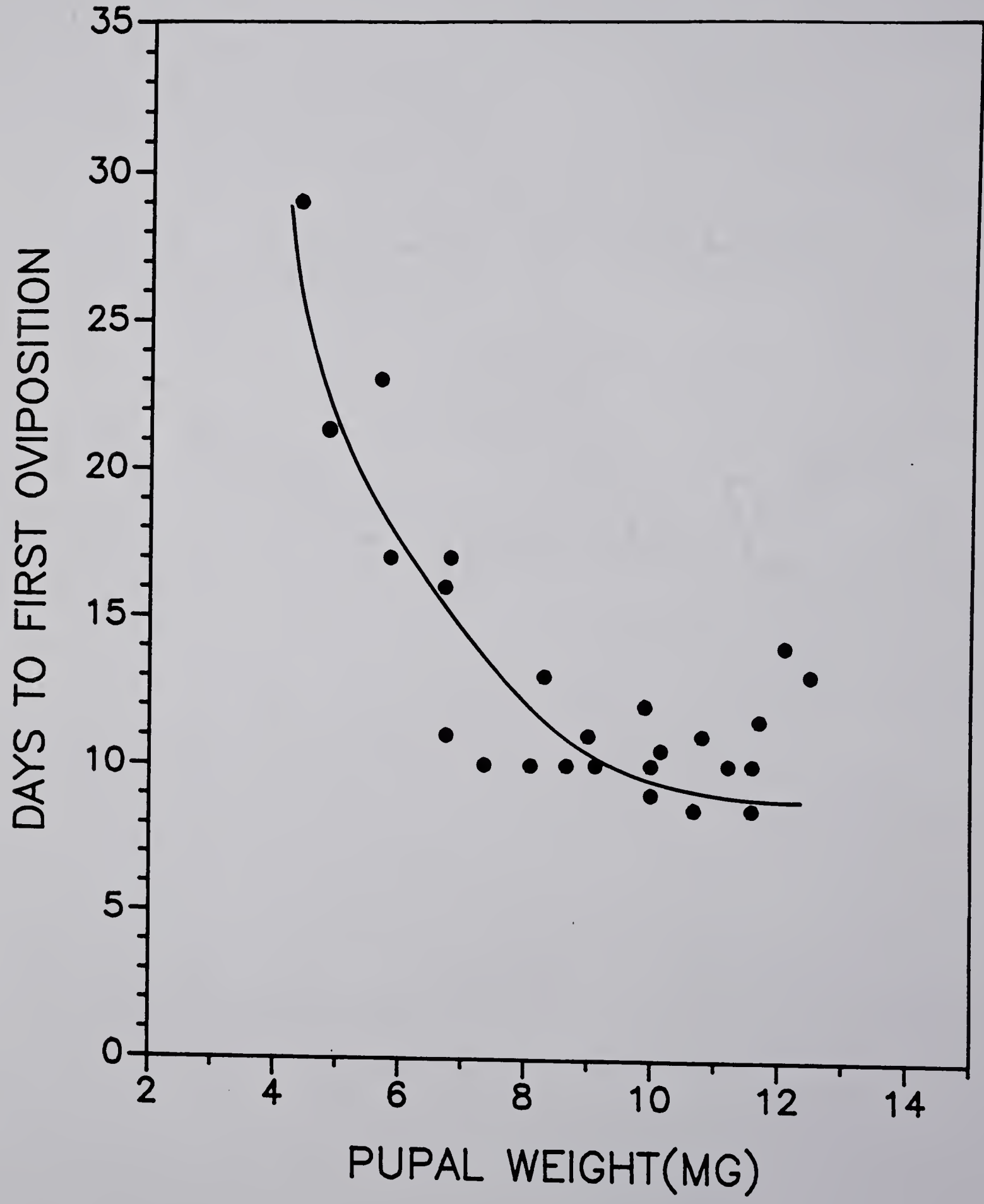
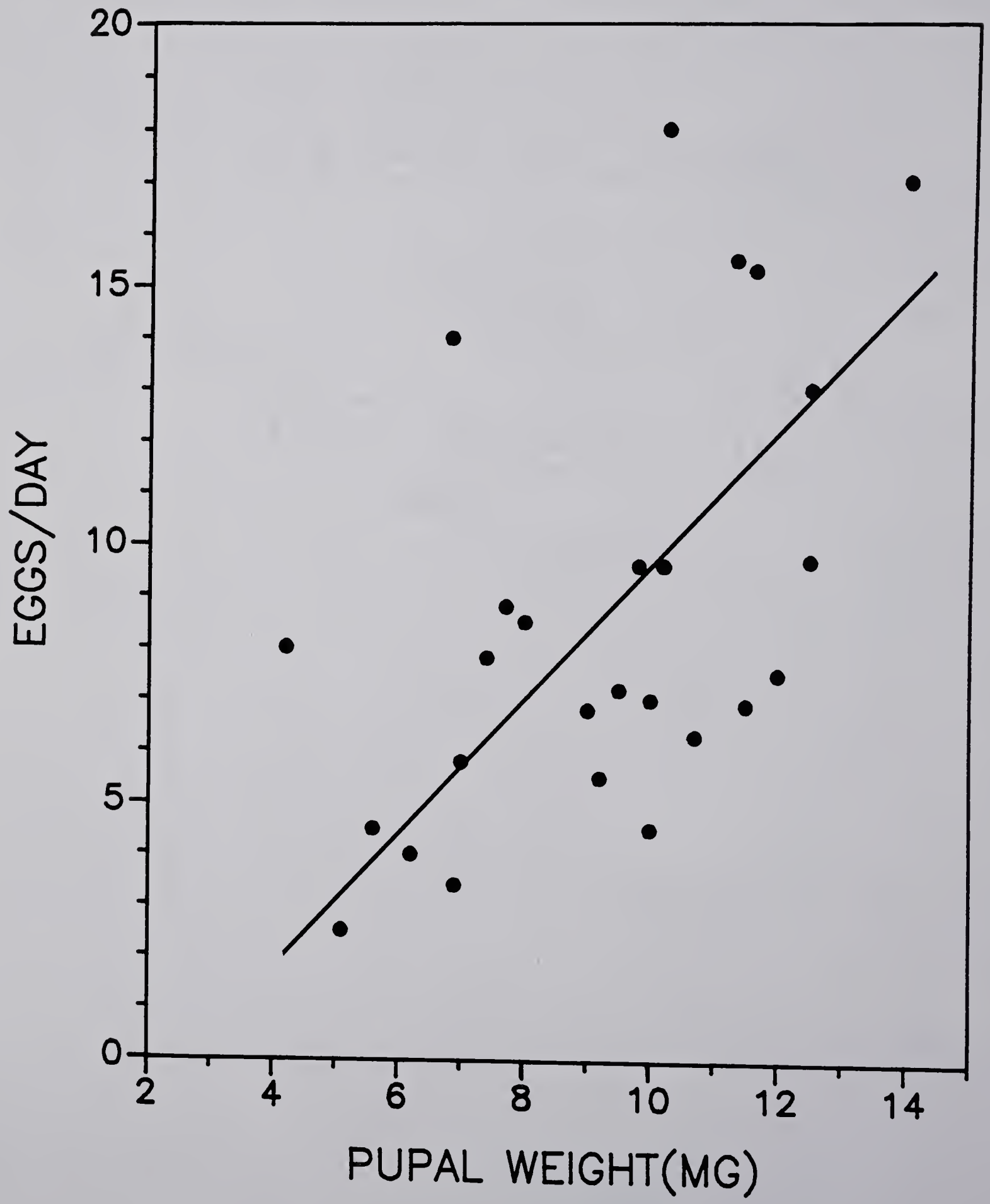

DAYS TO FIRST OVIPOSITION
35
30
25
20
15
10
5
0
2
4
6
8
10
12
14
PUPAL WEIGHT(MG)

Figure 8. Effect of R. pomonella pupal weight on average lifetime oviposition rate. The regression equation is $y = 1.25x - 3.38$ ($r^2 = .45$, N = 26).


20
15
10
5
0
EGGS/DAY
2
4
6
8
10
12
14
PUPAL WEIGHT(MG)

= .07) following removal of pupae from diapause conditions.

Laboratory studies of other tephritids have shown diverse effects of larval crowding on parameters of adult fitness, but none address competition in natural populations. In two Dacus species, the melon fly, D. curcurbitae, and the olive fly, D. oleae, adult longevity and fecundity were lower for small flies that had developed as larvae under crowded conditions than for larger flies that developed under less crowded conditions (Tsiropoulos and Manoukas 1977, Kawai 1981). Further, in D. oleae, smaller males were poorer mating competitors. Investigation of the Mediterranean fruit fly (Ceratitis capitata) showed that, like R. pomonella, total number of eggs laid was independent of pupal weight (Debouzie 1978).

Studies spanning most insect orders have demonstrated an influence of increasing larval density on certain fitness parameters of surviving individuals. Size or weight of adults has usually been positively correlated with total fecundity or rate of oviposition (Klomp 1964), as has been shown in coprophagous face flies (Moon 1980), the predatory stinkbug, Podisus maculiventris (Evans 1982), the agromyzid leafminers, Liriomyza trifolii (Parrella 1983) and Agromyza frontella (Quiring and

MacNeil 1984a), the Indian meal moth, Plodia interpunctella (Podoler 1974) and the ichneumonid parasitoid, Nemeritis canescens (Podoler 1974). Like R. pomonella, stunted individuals of some other species require an extended prereproductive period, as for example, in stinkbugs (Evans 1982) and face flies (Moon 1980). Moon (1980) hypothesized that prolonged maturation of stunted females suggests that females have emerged with a relative metabolic deficit from which they must recover by feeding before they are capable of completing the first gonadotrophic cycle.

Because R. pomonella exploits an ephemeral resource, delay in reproductive maturity may result in decline in female fitness. Annual observation of several Crataegus species demonstrates that only 2 1/2 - 3 weeks elapse from first egglaying by R. pomonella in green fruit to the time of fruit redness, when the majority of fruit are already infested. In this event, later maturing females and their larval offspring may be faced with extreme competition for oviposition sites or larval resources. As demonstrated above, only initial larvae in a fruit realize peak size and survival.

Finally, I found that stunted R. pomonella females deposit pheromone of either decreased quality or quantity as compared to larger conspecifics (see Chapter II).

Oviposition-deterring pheromone as a mediator of larval competition

Correlation of amount of pheromone deposited with larval resource requirements. For each fruit size assayed in the field cage, a single dragging bout was sufficient to deter most females from further egg-laying (Figure 9). This corresponds well with the previous finding that larvae survive maximally when alone in a C. mollis fruit, regardless of fruit size. Small, medium, and large fruit marked with the average amount of pheromone deposited by a female following a single egg-laying (1 dragging bout equivalent) were rejected just as frequently as fruit marked with 2 or 3 dragging bout equivalents.

In comparison to field results, lab bioassays of increasing dragging bout number revealed that female threshold level of sensitivity to pheromone was greatly increased under the less natural conditions: most females accepted fruit marked during a single dragging bout (Fig. 10). In fact, pheromone deterrence levels comparable to field levels were realized only at the highest pheromone concentration: 5 dragging bout equivalents/fruit. Because of this discrepancy, lab assays were of limited utility, and thus, were discontinued.

Females dragged their ovipositors for a

Figure 9. Field bioassay of R. pomonella acceptance of C. mollis fruit marked with different numbers of dragging bouts (= pheromone deposition following a single egg-laying). Small fruit = 12 mm diam, medium fruit = 15 mm diam, large fruit = 20 mm diam. Values above bars represent the number of female arrivals on each fruit treatment.

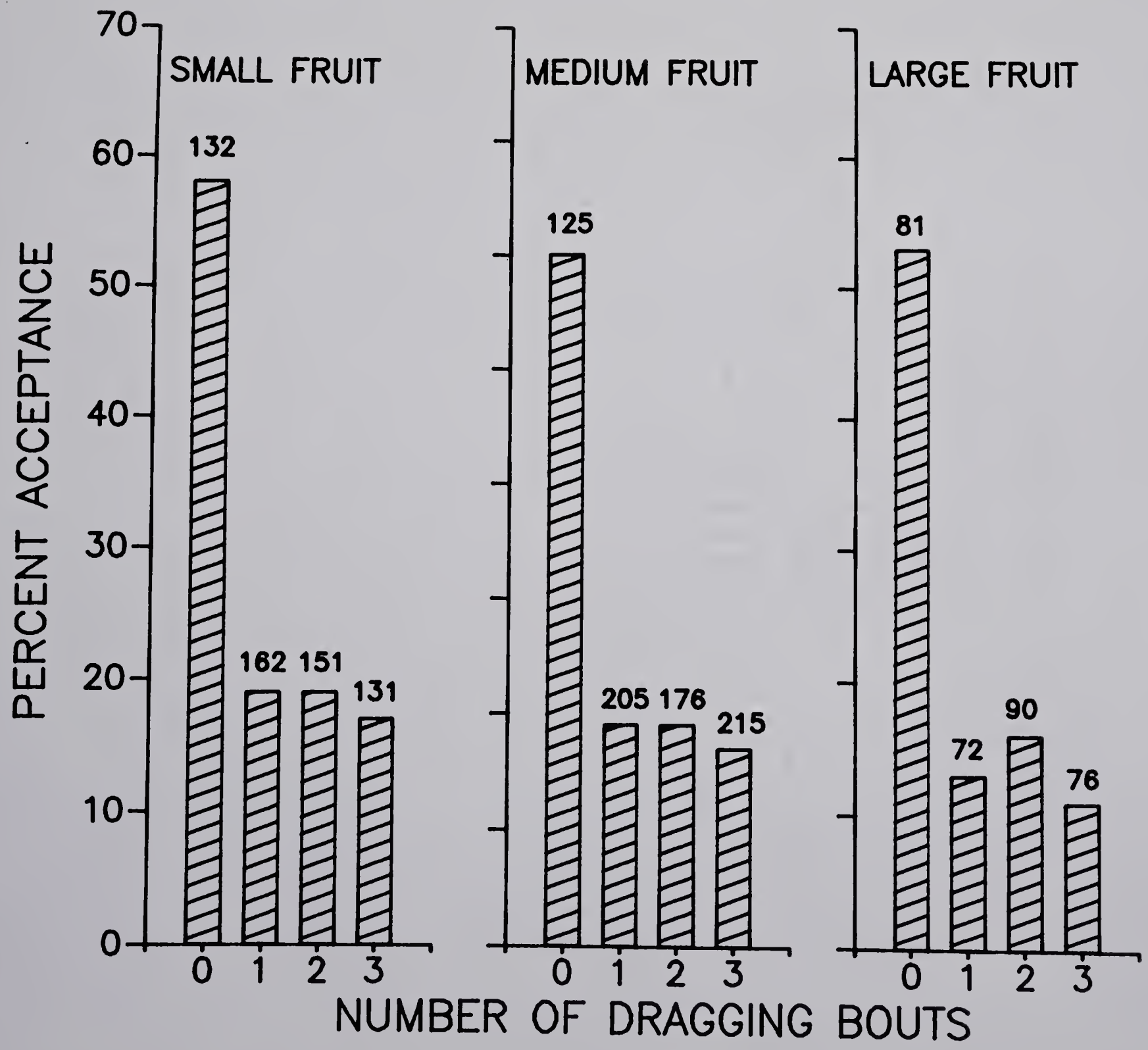
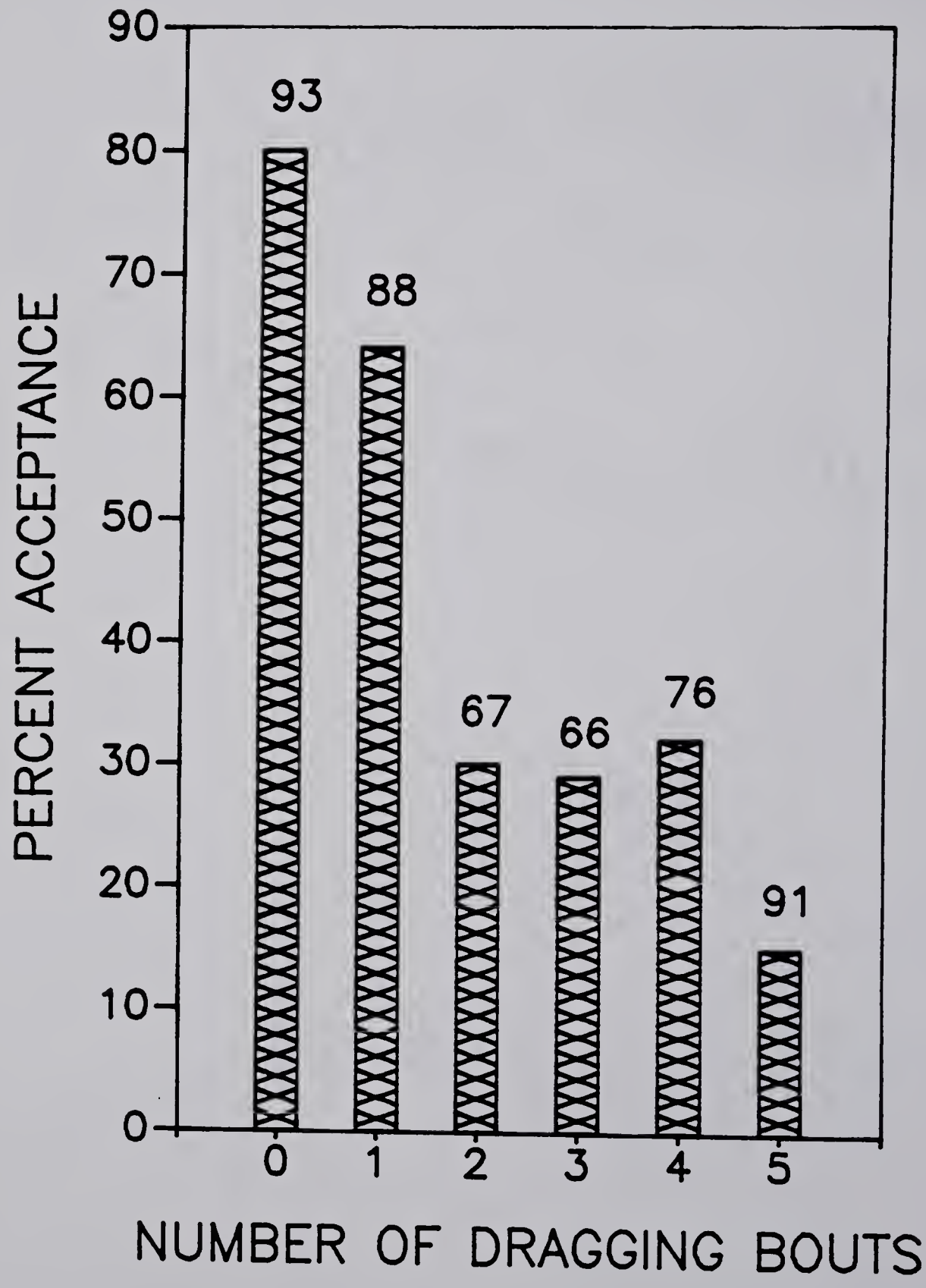

SMALL FRUIT
MEDIUM FRUIT
LARGE FRUIT
PERCENT ACCEPTANCE
70
60
50
40
30
20
10
0
132
162
151
131
125
205
176
215
81
72
90
76
0 1 2 3
0 1 2 3
0 1 2 3
NUMBER OF DRAGGING BOUTS

Figure 10. Laboratory bioassay of R. pomonella acceptance of C. mollis fruit (15 mm diam) marked with different numbers of dragging bouts (= pheromone deposition following a single egg-laying). Values above bars represent the number of female arrivals on each fruit treatment.


PERCENT ACCEPTANCE
90
80
70
60
50
40
30
20
10
0
93
88
67
66
76
91
0
1
2
3
4
5
NUMBER OF DRAGGING BOUTS

significantly longer time (at least 7 sec longer) and distance (at least 17 mm further) on large hawthorn fruit than on medium size or small fruit (Table 17) in both lab and field tests. Selective release of oviposition deterring pheromone has been demonstrated in the South American fruit fly, Anastrepha fraterculus, by fruit size (Prokopy et al. 1982a), in the trail laying behavior of Acanthomyops and Solenopsis ants by quality of food found (Hantgartner 1969a, 1969b), and in the egg marking behavior of Hylemya females by host plant species (Zimmerman 1980, 1982).

I do not know whether R. pomonella females assess fruit size during pre-oviposition or post-oviposition behavior, or both, but I suspect that as in A. fraterculus flies (Prokopy et al. 1982a), assessment occurs after oviposition when the fly is moving over the fruit surface while depositing pheromone. R. pomonella females perceive pheromone upon direct contact by sensilla on the tarsi (Prokopy 1981). Perhaps, while ovipositor dragging, females assess surface area, and therefore, host size on the basis of frequency of tarsal receptor contact with the newly deposited pheromone trail. Because large C. mollis fruit possess almost 3 times greater surface area than small fruit, the ratio of clean fruit surface area to pheromone-trail area would be far greater on large fruit.

Table 17. Effect of fruit size on duration and distance of ovipositor dragging (mean ± SE) by R. pomonella females on C. mollis fruit

Fruit size	Number of observations	Duration of dragging (sec)	Number of dragging circles*	Estimated dragging distance (mm)
small	195	23.06 ±1.74 a	3.00 ±.16 a	35.13 ±1.90 a
medium	162	24.64 ±1.25 a	2.84 ±.19 a	41.81 ±2.79 a
large	112	31.19 ±1.69 b	2.96 ±.18 a	58.79 ±3.55 b

*Number of times that a female dragged her ovipositor a distance that approximated the circumference of the fruit. This was estimated by eye.
Means in the same column followed by the same letter are not significantly different at the 5% level

A second possibility is that a fly may determine fruit curvature, and therefore size, simply as a function of its stance on the host, as is suggested for the Azuki bean weevil, Callosobruschus chinensis (Avidov et al. 1965b), or as a function of movement over the fruit surface. Such is the case in the polyphagous parasitoid, Trichogramma embryophagum, which assesses host size while antennating the host surface and adjusts the number of eggs deposited accordingly (Klomp and Terrink 1962). A third possibility is that a female may be able to discern completion of a dragging circle through perception of the surrounding environment. Such may be the case in hoverflies (Eristalis tenax), which forage for nectar in disc-florets of Aster (Gilbert 1983). Of all 3 mechanisms suggested, the latter seems least likely owing to the apparently random, zig-zag pattern of the R. pomonella dragging path.

It could be adaptively advantageous for a female to drag her ovipositor longer on a large than a small C. mollis fruit: if a female drags fewer than 3 circles on a large fruit, deterrence of arriving females is not realized (Table 18). The reason why the same length of pheromone trail on a small fruit and a large fruit results in deterrence on the former and no deterrence on the latter is related to the fact that a female must cross a pheromone trail a given number of times (ca. 6 for a small

Table 18. Percentage of R. pomonella females accepting large (20 mm diam) C. mollis fruit marked during incomplete dragging bouts or 1, 2, or 3 complete bouts* in field bioassays.

Number of dragging circles**	Number of dragging bouts	Number of female arrivals on fruit	% boring attempts
0	0	61	53 a
1	1/3	60	47 a
2	2/3	42	45 a
3	1	116	13 b
6	2	80	16 b
9	3	71	11 b

* A "dragging bout" = pheromone deposition following a single egglaying

** Number of times that a female dragged her ovipositor a distance that approximated the circumference of the fruit

Values in the same column followed by the same letter are not significantly different at the 5% level according to a G test

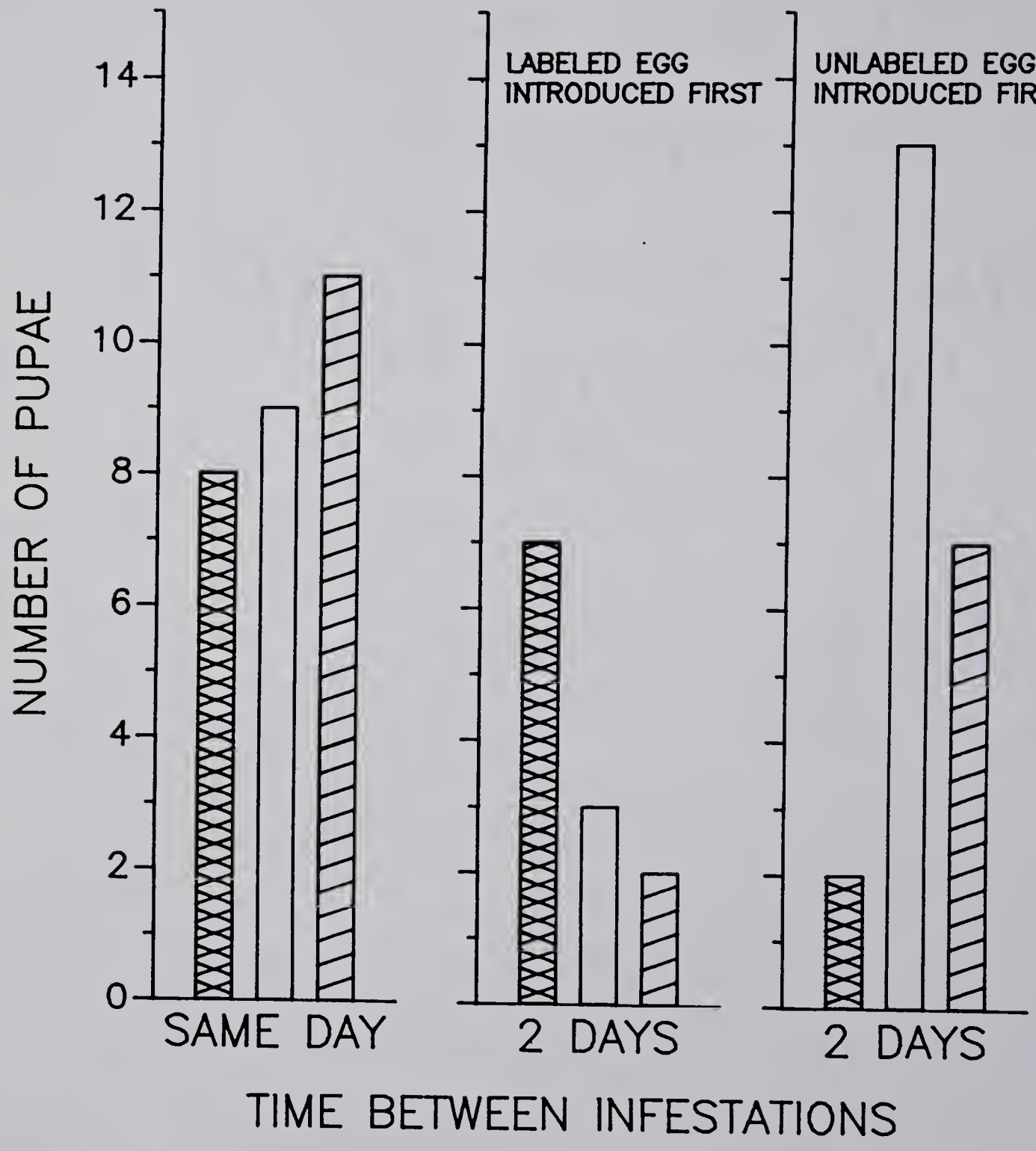
fruit) during pre-oviposition fruit inspection before fruit rejection normally is manifested (Prokopy 1981). The 3-fold greater surface area of a large fruit compared with a small one results in a much less rapid increase in the ratio of pheromone-marked fruit surface area to clean fruit surface area each time a female completes a dragging circle on a large as compared to a small fruit.

For many other insect species that utilize host discrimination mechanisms, results demonstrate or suggest that both the amount of deterrent stimulus deposited and the amount of stimulus required to elicit deterrence are linked with the host's carrying capacity. Numerous examples of such a phenomenon exist in those parasitic Hymenoptera whose larvae are solitary: a single marking bout by a female effects host discrimination (van Lenteren 1981; Salt 1961). Such appears to be the case also in other tephritid species ((e.g. Paraceratitella eurycephala, which infests mistletoe fruit (Fitt 1981), and Rhagoletis alternata, which infests rose hips (Bauer 1983)), in the sorghum shootfly, Atherigona soccata (Raina 1981a, 1981b), and finally, in Battus pipevine swallowtail butterflies, where females utilize visual cues to avoid already occupied host plants, which often have insufficient foliage to support the growth of even a single larva (Rausher 1979).

Importance of a developmental headstart for a larva. Data in Fig. 11 suggest that in double infestations of C. oxyacantha fruit, a 2-day headstart is an important factor determining the "winning" larva's identity. However, a simple interpretation of these data is not possible because there were 3 distinct ^{32}P categories into which winning larvae fell: unlabeled ($<$ 20 CPM), labeled ($>$ 100 CPM), and intermediate (40-70 CPM). Eighty-nine percent of all larvae fell into these categories. It is possible that intermediate-level larvae arose as a result of unlabeled larvae either accidentally or aggressively consuming labeled rivals. Alternatively, unlabeled larvae could have been contaminated through consumption of excretory products or exuviae of labeled larvae. This is unlikely, however, as preliminary studies demonstrated that the majority (ca. 85%) of a labeled larva's ^{32}P content remained incorporated in body tissues through completion of its development.

If intermediate-level larvae represent contaminated unlabeled larvae, then the majority of winning larvae (71%) in simultaneous infestations consists of unlabeled larvae. This suggests that the radiolabel may have rendered a larva less able to compete and highlights the intensely competitive conditions engendered by

Figure 11. Effect of 2-day headstart in determining the "winning" R. pomonella larva's identity for double infestations of Crataegus oxyacantha fruit. P categories are unlabeled (< 20 CPM), labeled (> 100 CPM), and intermediate (40-70 CPM). The number of simultaneously infested fruit was 31, of fruit with a labeled egg introduced first was 14, of fruit with an unlabeled egg introduced first was 25. Some fruit produced no larvae.


NUMBER OF PUPAE
0
2
4
6
8
10
12
14
LABELED EGG INTRODUCED FIRST
UNLABELED EGG INTRODUCED FIRST
SAME DAY
2 DAYS
2 DAYS
TIME BETWEEN INFESTATIONS

simultaneous infestations in severely resource-limited hosts. However, this also highlights the advantage gained by a larva having a headstart, as the presumed less-competitive labeled larva won in a substantial majority of cases when they were introduced 2 days prior to an unlabeled competitor (Fig. 11).

Additional data concerning single and double infestations in C. oxyacantha fruit are presented in Table 19. Most larvae (ca. 70%) growing singly in these fruit completed development successfully. Regardless of treatment, only a single larva completed development in all double infestations, save 6%, where no larvae survived. There was no significant difference in pupal weight or larval development time between any of the fruit treatments, either double or single larval infestations. However, the larvae in all treatments required nearly 2 times longer to complete development and the pupae were 30-50% lighter than individuals that had developed in C. mollis fruit. Inspection of fruit at the end of the experiment revealed that the flesh lying between the seed and the leathery skin had been entirely hollowed out, suggesting that larvae developing in C. oxyacantha fruit required extended development time to procure as much of the fruit's meager resources as possible.

Table 19. Percent R. pomonella larval survivorship to puparial formation, mean pupal weight (mg ± SE), and mean larval development time (days ± SE) in singly and doubly infested C. oxyacantha fruit. Labeled eggs originated from females that had been injected with ^{32}P.

fruit treatment	N	% larvae surviving to puparial formation	pupal weight	larval development time
Single infestations				
Unlabeled egg only	45	73	5.79 ±1.3 a	26.7 ±2.4 a
Labeled egg only	17	71	6.31 ±1.3 a	26.0 ±3.8 a
Double infestions				
A labeled and an unlabeled egg introduced on same day	31	45	6.14 ±1.1 a	27.9 ±2.5 a
2-day interval separating introductions:				
1st: labeled egg				
2nd: unlabeled egg	14	46	6.39 ±1.6 a	28.3 ±2.1 a
2-day interval separating introductions:				
1st: unlabeled egg				
2nd: labeled egg	25	49	5.68 ±1.8 a	27.8 ±2.8 a

Means in the same column followed by the same letter are not significantly different at the 5% level

Mechanisms of competition among larvae

There are 2 types of competition among animals: interference and exploitation (Miller 1967). These interactions may also be referred to as contest and scramble competition, respectively (Nicholson 1954). Interference occurs where a competitor's activities either directly or indirectly limit its rival's access to a resource. This includes such phenomena as territoriality, cannibalism, or physiological suppression (Miller 1967). This mechanism allows at least one individual to obtain sufficient resources to meet its growth requirements (Beaver 1973). In contrast, exploitation-type competition involves joint utilization of a limited resource, with each individual gaining a proportion of resource corresponding to its exploitative ability (Miller 1967). As noted by Klomp (1964), as density increases and exploitation-type competition intensifies per unit of resource, an increasing part of the resource may be wasted. In the extreme case, the entire resource may be wasted as a result of "collective suicide" and 100% mortality of all competitors (Miller 1967). Elements of both interference and exploitation competition often interact together within crowded populations (Miller 1967).

The evidence for apple maggot larvae implicates an

interference component. Although most C. mollis fruit appear to possess ample resources for development of 2 or 3 larvae, there was a severe decline in larval survivorship in doubly and triply infested fruit, with most fruit producing only a single larva. The results of the radiolabeling experiment using C. oxyacantha as a host likewise suggest an interference component.

As in R. pomonella, older and larger first-introduced Drosophila melanogaster larvae in a laboratory medium are competitively dominant over later-introduced younger and smaller larvae (Gilpin 1974). Several possibilities are offered by Gilpin to explain this finding. First, the headstart awarded initial individuals may give rise to exhaustion of the resource or the superior part of it. An exploitation-type interaction of this sort has been suggested for early and late hatching cohorts of treehole mosquitoes, Aedes triseriatus, developing under low food conditions (Lidvahl 1982). Apparently, because large, early hatching larvae can more efficiently exploit a wide range of food particles, they impose an adverse effect on cohorts hatching a week later. This type of exploitation interaction could indeed occur in R. pomonella developing in C. oxyacantha fruit, where the oldest larva could monopolize the meager fruit resources. However, it does

not explain how only a single R. pomonella larva was able to complete development in nearly all simultaneously doubly-infested C. oxyacantha fruit. Nor does it explain the preponderance of cases where only a single larva developed in multiply infested large C. mollis fruit. Second, Gilpin suggests that older larvae may be able to poison or in some way physiologically suppress younger larvae. In D. melanogaster, burrowing third instar larvae may release metabolites to the medium's surface, where first and second instars are confined, thus suppressing the younger instars' growth. Budnic and Brncic (1974, 1976) found that older D. pavani larvae produce waste or food breakdown products that inhibit growth of younger larvae, but do not adversely affect older larvae. Fitt (1983) found a similar phenomenon in the tephritids, Dacus tyroni and D. jarvisi. Perhaps, differential survival according to size results from the fact that surface area to body ratio is proportionally higher in smaller individuals. Such differential survival of various-aged larvae under stressful conditions is reminiscent of Fisher's (1961, 1963) classic observations on the solitary ichneumonid parasitoids Nemeritis and Horogenes. If the age difference in these parasitoids was more than 50 hr, then older larvae were able to suppress younger ones by utilizing all available oxygen in the host. Finally,

Gilpin suggests that dominance by older larvae may simply be a size phenomenon: younger larvae may sustain more serious injury or die during accidental larval collisions. There is no evidence supporting this possibility in R. pomonella, but such has been shown in bark beetles, where first-emerging, large larvae inadvertently eat through later-emerging smaller larvae (Beaver 1974).

Large larvae may achieve dominance by physically attacking and destroying younger, smaller larvae. In tephritids, observations of larval fighting and aggressive clawing with the mouthhooks have been reported for at least two species: R. cerasi (Katsoyannos et al. 1977, unpublished data), and Dacus oleae (Moore, cited in Monro 1967). Attacks by older larvae have been described for many solitary parasitoids. On the other hand, battles in some parasitoid species are restricted to first instars which possess specialized sickle-shaped mandibles for fighting. Similarly, 1st and 2nd instars of the alfalfa blotch leafminer are aggressively cannibilistic, whereas 3rd instars are not (Quiring and McNeil 1983b).

It is not known if aggressive encounters take place among rival R. pomonella larvae, but if they do occur, size and consistency of the host fruit could be important to encounter frequency. In very small fruit, and in fruit where decay and liquification are advanced, rapid larval

movement and encounter frequency may be enhanced. Salt (1961) questions how supernumerary parasitoid larvae, which are miniscule in comparison to their hosts, meet for aggressive encounters. He suggests that parasitoid larvae may actively search for one another or may aggregate in certain locales within hosts. Both mechanisms may enhance larval encounter and elimination rates. Aggressive searching has been observed in alfalfa blotch leafminers, wherein, upon detection of a mine, a larva proceeds to move rapidly up the mine, attacking the mine's occupant from the rear (Quiring and McNeil 1983b).

Process of resource exploitation

My findings show that R. pomonella exhibits several well-developed mechanisms that allow efficient utilization of limited host fruit resources. At low and moderate fly population densities, larval competition can be circumvented by adult recognition of already occupied resources via oviposition-deterring pheromone signals. The result of such host discrimination may be even dispersion of eggs among available host fruit (see Chapter V). If pheromone activity decays prior to completion of larval development, or is reduced as a result of heavy rains, R. pomonella is able to detect the presence or effects of second and third-instar larvae (Chapter III),

an additional means of host discrimination. When fly population density is high or host discrimination mechanisms break down, females may oviposit randomly (Reissig and Smith 1978, Chapter V). Such random egglaying may result in the overloading of fruit. Even then resources may not be wasted because the development of at least one larva is assured, probably due to interference competition among larvae.

A similar scenario may exist for the cowpea weevil, Callosobruchus maculatus, (Utida, cited in Giga and Smith 1981) in its exploitation of available peas or beans, and has been proposed for Rhagoltis alternata infesting rose hips (Zwolfer 1982, Bauer 1983).

Evolution of host discrimination

The impact of competition on the intraspecific dynamics of insect populations is an area of controversy (see review in Denno and McClure 1983). Some believe that among phytophagous insects, intraspecific competition is only of minor importance (Hairston et al. 1960, Klomp 1964, Faeth and Simberloff 1981). Indeed, Dethier (1959) states that "those insects whose larvae feed on plants do not increase to the larval food limit except in sporadic and unusual cases."

Such relegation of intraspecific competition to an

insignificant role in herbivorous insect population dynamics seems inappropriate for at least some insect-plant systems, particulary in those insects that possess sophisticated host discrimination mechanisms allowing avoidance of oviposition at sites already occupied by conspecifics. In such species, including many frugivorous tephritids and granivorous beetles (see Prokopy et al. 1984), intraspecific competition not only occurs in natural populations, but appears to be a key element influencing the evolution of oviposition behavior and resource exploitation strategies (e.g. Whitham 1978, Quiring and McNeil 1984b).

Certain features of a species' biology may correlate with both intraspecific competition and host discrimination. For example, Rausher (1979) and Thompson (1983) suggest simply that severe competition as well as the ability to assess egg load will be likely in species whose hosts are small relative to the requirements of developing immatures. Such is the case for pipevine swallowtail butterflies (Battus philenor) and sorghum shootflies, whose host plants often do not have enough foliage to support the development of even a single larva to maturity (Rausher 1979, Raina 1981a, 1981b). Thompson (1983) further suggests that insects feeding on seasonally restricted, ephemeral plant parts such as flowers,

meristems, and fruit, are more likely to develop host discrimination abilities than those feeding on more persistent parts such as roots and leaves. Along this line, Benson (1978) and Gilbert (1982) suggest that intraspecific competion may be especially intense when insects exploit rare resources that have low recovery ability following herbivore attack. This speculation is based primarily on studies of neotropical heliconid butterflies, which oviposit only on fresh shoots of scattered passion vine species. Finally, Prokopy (1981) and Szentesi (1981) designate a suite of traits that may increase the probability of potentially adverse encounters as well as the probability of egg load assessment mechanisms. First, encounters may be more common in those species whose immatures must complete development at constricted sites (such as buds and fruit) selected by their parent and who have limited or no ability to exploit alternative sites. Second, encounter frequency may be further elevated if the species exhibits monophagous-oligophagous (specialist) feeding habits involving resources which are relatively predictable in space and time. Many frugivorous tephritids exhibit this suite of traits.

C H A P T E R V

DISTRIBUTION PATTERNS OF *RHAGOLETIS POMONELLA* EGGS IN HAWTHORN (*CRATAEGUS*)

Introduction

Investigation of the dispersion of an insect population may reveal mechanisms governing dispersion, such as patterns of resource exploitation (e.g. van der Meijden 1976), competitive interactions (e.g. Holter 1982), patchiness in resource quantity (e.g. Drake 1983) or quality (e.g. Carne 1965, Myers *et al*. 1981, Stamp 1982) or interactions between natural enemies and prey (e.g. Morrison and Strong 1981, Heads and Lawton 1983). Further, analysis of the spatial distribution of an insect pest may be critical in development of reliable sampling regimes for management programs.

Most populations are aggregated; random or uniform dispersions are less commmonly reported (Taylor 1961, 1984; Southwood 1978, Cornell 1982). Uniform dispersion is likely in species wherein individuals discriminate against previously utilized resources. For example, visually mediated recognition of utilized oviposition

sites has been demonstrated in Battus philenor, the pipevine swallowtail (Rausher 1979), Pieris sysymbrii (Shapiro 1981), Heliconius cydno (Williams and Gilbert 1981), and Anthocaris cardamines (Wicklund and Ahrburg 1978). Only in the case of A. cardamines, however, has egg avoidance been experimentally shown to result in uniform dispersion of eggs (Shapiro 1980). Chemically mediated recognition of resource sites has been reported for a diverse array of insects, and in a number of instances, uniform dispersions have been reported as well. This includes the discovery of uniform egg dispersion in numerous parasitoids (Vinson 1976), Hadena moths (Brantjes 1976), the anthomyiid fly, Hylemya spp. (Zimmerman 1979), the bruchid beetles, Callosobruchus chinensis, C. maculatus, and Acanthoscelides obtectus (Avidov et al. 1965b, Umeya and Kato 1970, Mitchell 1975), the cabbage seed weevil (Ceutorhynchus assimilis) (Kozlowski et al. 1983) and at least 20 Tephritid fruit flies (reviewed in Prokopy 1976, Fitt 1983). In these species, the immatures are sedentary or poorly vagile and utilize small, discrete resource units in which food depletion and competitive interactions are likely if overloading occurs. Thus, distribution of eggs or larvae among available food units may be critical to efficient resource exploitation.

Prokopy (1972) reported that immediately following

egglaying in a host fruit, a female apple maggot fly, Rhagoletis pomonella, drags her extended ovipositor over the fruit surface and deposits a trail of oviposition-deterring pheromone (ODP). This pheromone elicits dispersal of arriving conspecifics away from marked hosts. In the previous chapter, I showed that on Crataegus hawthorn fruit (the native host of the fly) R. pomonella exhibits a very sensitive host discrimination ability: a single ODP deposition bout following egglaying in a fruit was sufficient to deter oviposition. Further, in Chapter III, I showed that the pheromone was moderately stable over time and in rainfall. For these reasons, I anticipated that in nature, R. pomonella egg dispersion was likely to be uniform. Previous research on R. pomonella egg dispersion has been inconclusive: two studies conducted on apple demonstrated a uniform dispersion of eggs within regions of the crown of individual trees (LeRoux and Mukerji 1963, Cameron and Morrison 1974) whereas a third, conducted on hawthorn, revealed a random dispersion of eggs among fruit (Reissig and Smith 1978).

I investigated the dispersion pattern of R. pomonella eggs among hawthorn fruit within trees and within portions of trees. The study was begun upon observation of the first oviposition puncture and was

continued throughout the fruit ripening season until fruit abscission.

Materials and Methods

Field observations of egg dispersion pattern among fruit were conducted during the summer of 1982 on two large (6 m tall) Downy hawthorn trees (Crataegus mollis) located on the University of Massachusetts campus. Both trees were adjacent to a third central tree and bore ca. 30,000 fruit in clusters of 5-15 fruits/cluster.

To determine egg dispersion of R. pomonella within the tree crown and to compare overall egg distribution in portions of trees, I followed the scheme established by LeRoux and Reimer (1965) and divided the trees into 8 sampling sections: top and bottom half; north, south, east and west quadrants. Rather than select fruit randomly from each of these sections (as did Leroux and Reimer), fifteen branchlets throughout each section were flagged randomly and on each sampling occasion, a single fruit was drawn from each of these same flagged branchlets. I was unable to conduct a random sampling program because throughout each tree, isolated clusters (1% of all fruit on the trees) on certain branchlets had ripened inordinately early, while all other fruit on the

tree were hard and green. This uneven ripening appeared to be due to disease or branchlet breakage. Because many mature R. pomonella females were present in the trees before I began sampling, each prematurely ripened fruit was already heavily infested. On August 16, when egg numbers in fruit on other branchlets was low (0.3/fruit), the mean number of eggs per fruit on these branchlets was 3.5, with some hawthorns containing over 10 eggs. For this reason, I excluded these branchlets from the sampling program. I did monitor egg densities on these excluded branchlets by regularly sampling fruit from them.

Hawthorns were collected 12 times from both trees from August 12 to September 24 every 2-4 days, except at the end of the season, when 1 week elapsed prior to the final fruit collection of September 24. Each sampled fruit was examined and dissected in the laboratory under a binocular microscope and the numbers of R. pomonella oviposition punctures and eggs were recorded. Hatched egg cases were recorded as "eggs." On each sampling date, 240 fruit were examined. A total of 2880 fruit was examined over the season.

Egg dispersion among fruit for each sampling day was analysed using the Index of Dispersion (Southwood 1978, Elliot 1982). This measure is simple to apply and understand, is only slightly biased by density and is the

most direct measure of dispersion (Myers 1978, Meyers and Harris 1980). Elliot (1982) cautions that this measure may be too insensitive to detect non-randomness in some cases of low counts or small samples ($n < 30$).

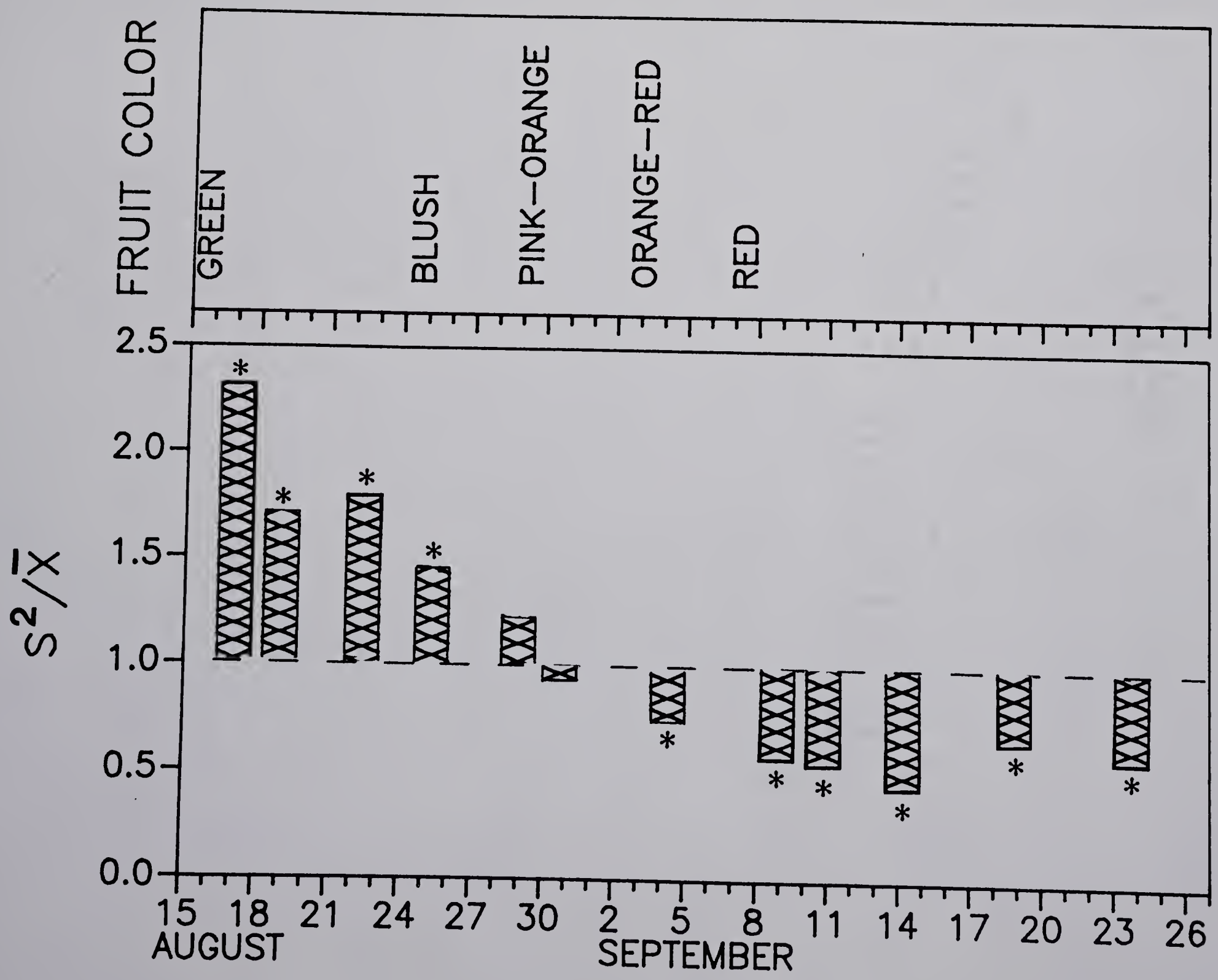
An analysis of variance was made of all egg counts on log (x+1) transformed data to determine differences in the spatial distribution of eggs within and between trees. Where comparison of means was appropriate, values were separated by Student-Newman-Keul's procedure at the 5% level of significance.

Results

Dispersion of eggs among fruit

The dispersion of *R. pomonella* eggs among host fruit changed over the season, showing 3 distinct phases in dispersion pattern (Fig. 12). Eggs were aggregated in fruit at the beginning of the season: samples collected on August 17, 19, 23 and 26 each had variance to mean ratios significantly greater than 1. This conclusion is supported by the fact that, for each of the four samples, the observed egg dispersion did not depart significantly from the negative binomial distribution (August 17, χ^2 = 2.99; August 19, χ^2 = 8.44; August 23, χ^2 = 3.92; August

Figure 12. R. pomonella egg dispersion pattern among C. mollis fruit during August and September, 1982. On each sampling day 240 fruit were examined. Histogram bars represent variance (s^2) to mean ($\bar{x}$) ratios for each sampling day. Ratios greater than 1 represent an aggregated dispersion, those less than 1 represent a uniform dispersion, and those = to 1 represent a random dispersion. Stars above bars indicate significant departure from a random dispersion at the 5% level according to the Index of Dispersion.


FRUIT COLOR
GREEN
BLUSH
PINK–ORANGE
ORANGE–RED
RED
$S^2/\bar{X}$
2.5
2.0
1.5
1.0
0.5
0.0
15 18 21 24 27 30 2 5 8 11 14 17 20 23 26
AUGUST
SEPTEMBER

26, χ^2 = 6.09). Egg clumping was most evident on the first sample date, August 17, when 50% of infested fruit contained multiple eggs, even though 85% of the fruit remained uninfested (Fig. 13). Many of the multiply infested fruit contained eggs clustered at a single site on the fruit. On August 17, all sampled fruit were hard and green. By August 23 at least 1/2 of the fruit had an orange blush, and by August 26, all fruit had a blush.

Eggs were randomly dispersed among fruit collected on August 29 and 31 when most fruit were pink-orange. Variance to mean ratios which did not depart significantly from 1.

Eggs were uniformly dispersed among fruit sampled on September 4, 9, 11, 14, 17, and 24. More fruit contained 1 egg than would be expected if the eggs were dispersed randomly, as determined by comparison with the expected Poisson distribution (Table 20). In fact, among ripe infested fruit, approximately 75% contained a single egg. At the beginning of September, most fruit had turned orange-red and by September 9, all fruit were red, soft, and "ripe".

For samples collected from August 17 to September 4, the total percentage of infested fruit and the mean number of eggs per fruit increased in a curvilinear fashion from 15% to 63% and from 0.29 to 0.85, respectively (Fig. 13,

Figure 13. Seasonal changes in percentage of sampled C. mollis hawthorn fruit infested with R. pomonella eggs, and percentage of observed oviposition punctures that contained an egg. On each sampling date, 240 fruit were examined.

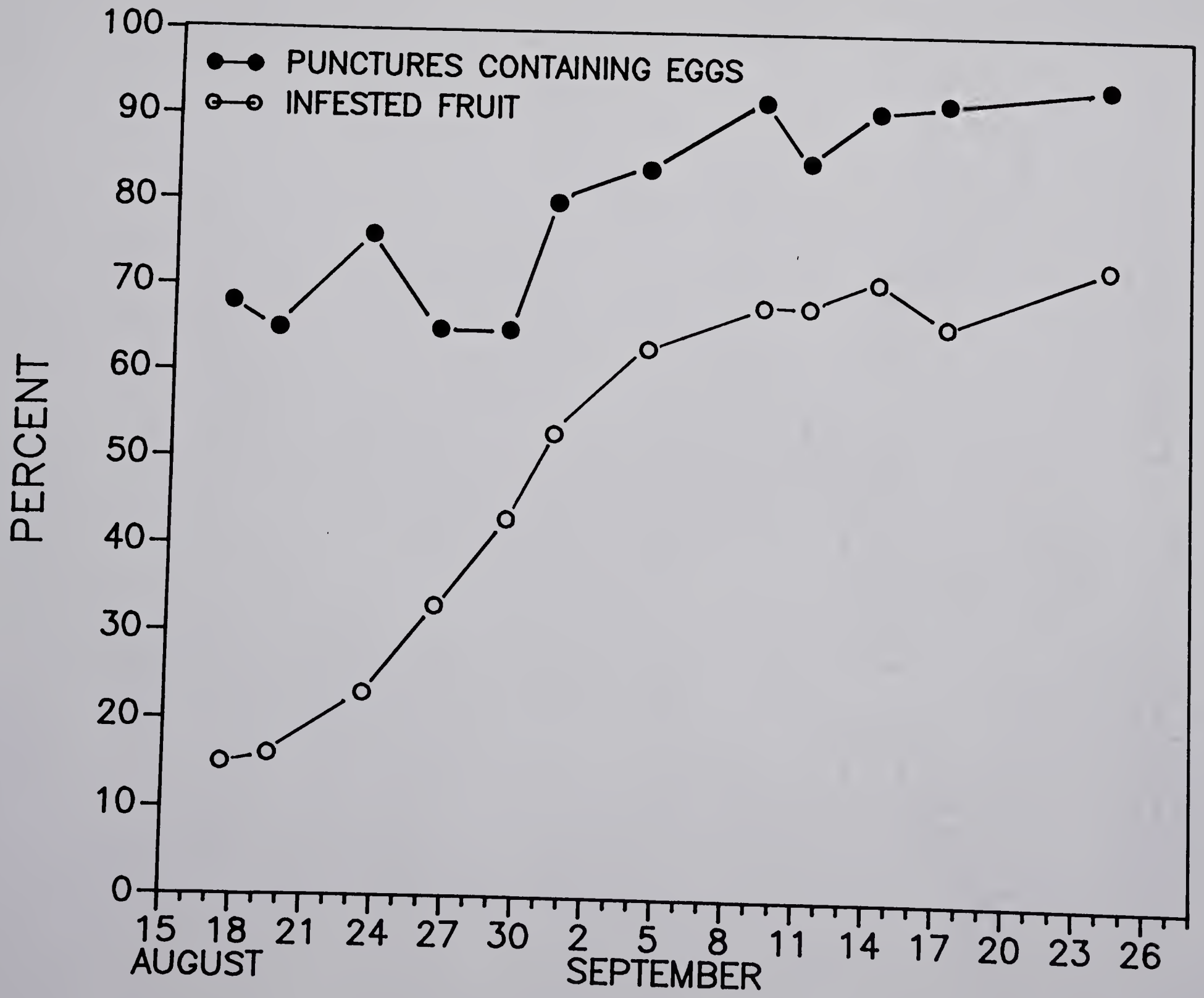

PUNCTURES CONTAINING EGGS
INFESTED FRUIT
PERCENT
100
90
80
70
60
50
40
30
20
10
0
15 18 21 24 27 30 2 5 8 11 14 17 20 23 26
AUGUST
SEPTEMBER

Table 20. Counts of number of R. pomonella eggs per C. mollis fruit. On each sample date, 240 fruit were examined.

Day	Number of eggs/fruit								Total no. eggs counted
	0	1	2	3	4	5	$\bar{X}$	s^2	
Aug 17	204	18	8	6	3	1	.28	.64	69
Aug 19	202	24	7	6	1	0	.24	.42	60
Aug 23	186	34	11	3	4	0	.34	.61	81
Aug 26	160	58	19	3	1	0	.43	.58	109
Aug 29	138	69	25	6	2	0	.62	.72	145
Aug 31	115	106	12	4	2	0	.63	.56	150
Sept 4	89	109	34	6	2	0	.85	.66	203
Sept 9	79	119	34	8	0	0	.88	.56	211
Sept 11	77	114	43	5	0	0	.90	.59	215
Sept 14	70	133	35	7	0	0	.91	.53	219
Sept 17	82	118	32	6	2	0	.86	.62	206
Sept 24	64	137	32	5	2	0	.93	.56	224

Table 20), and leveled off at ca. 70% infested fruit and 0.90 eggs per fruit. After this time, no substantial increases in these values were observed. The percentage of infested fruit leveled off at ca. 70% and the mean number of eggs per fruit leveled off at ca. 0.90.

From August 17 until August 29 (when fruit were pink-orange), the percentage of punctures containing eggs was ca. 65%. This value increased in subsequent samples and leveled off at ca. 90% when all fruit were ripe (September 9) (Fig. 13).

Samples of prematurely ripened fruit that had been excluded from the general sampling scheme contained a mean of 4.86, 4.89, 3.05, and 2.22 eggs per fruit on August 17, 19, 23 and 26, respectively. In several cases, as many as 9 eggs were observed in a single fruit. Egg numbers in these fruit probably decreased over time because the ripest and most heavily infested fruit prematurely abscised from the tree.

Distribution of eggs within and between trees

The distribution of R. pomonella eggs between crown levels and between trees changed over the 1982 summer season. Whereas there were no differences in total egg number in Tree 1 vs. Tree 2 during the month of August, during September, egg density was significantly higher in

Tree 2 on all sampling occasions, except September 9 and September 24 (Table 21). Similarly, for combined data, differences in egg density between crown levels became more pronounced as the season progressed. Except for samples collected on August 17, 19 and 26 there were consistently more eggs in the top half of the crown; in the majority of cases these differences were statistically significant (Table 21). Scrutiny of single tree data (Fig. 14) and analysis of variance for tree x level interactions (Table 22) reveal that in September, this crown level difference was salient in Tree 2, and was much less pronounced or nonexistent in Tree 1.

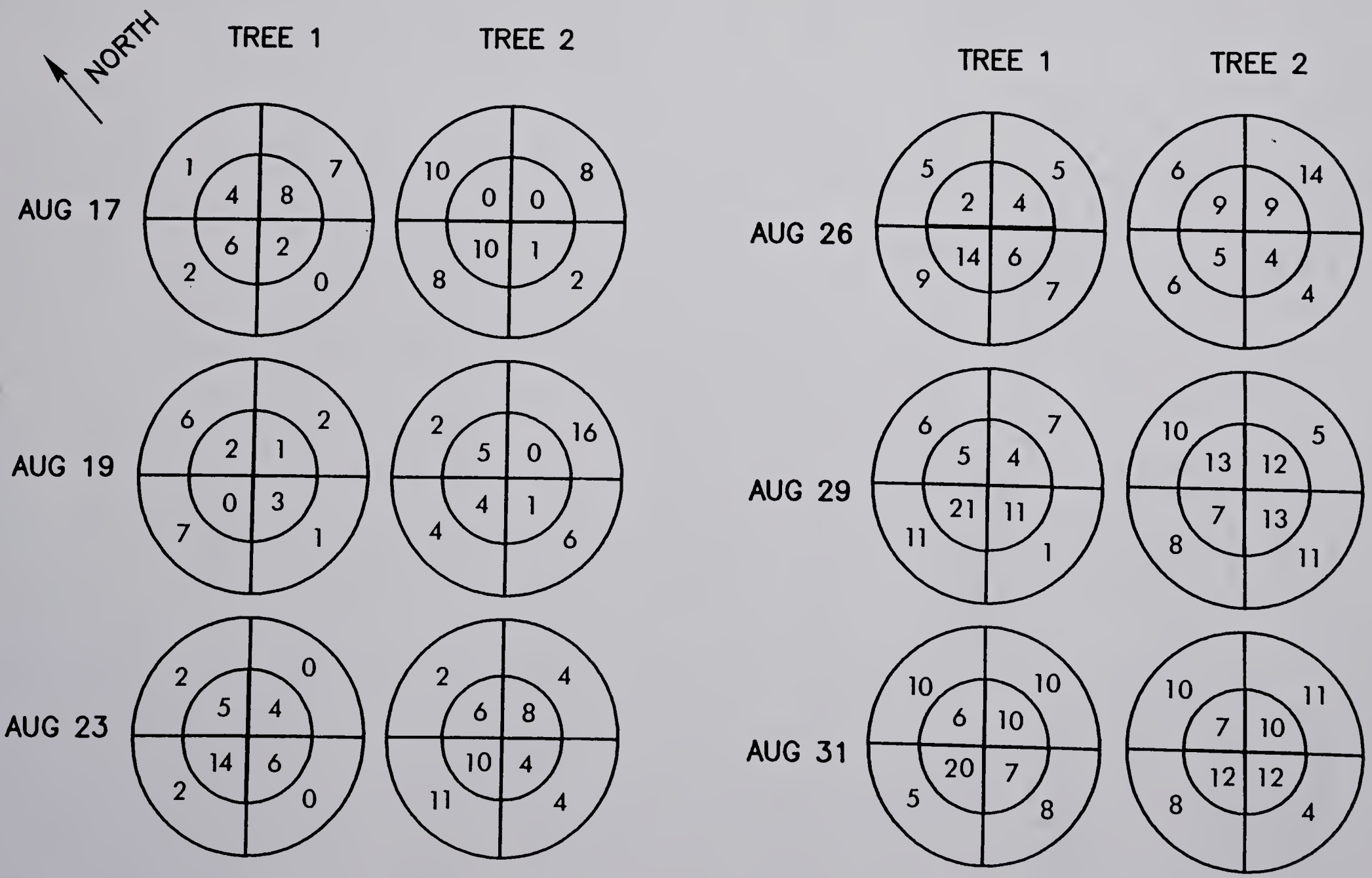
There was no evidence that egg distribution was affected by cardinal aspect of the tree crown (Table 21). The single exception to this occurred on August 23, when significantly more eggs were collected in samples from the west quadrant. In general, following fruit ripening, egg density was similar among north, south, east and west quadrants (Fig. 14).

Discussion

Dispersion of eggs among fruit

The dispersion pattern of R. pomonella eggs among host fruit changed over the season, showing first an

Figure 14. Total number of R. pomonella eggs counted for each C. mollis tree subsection. Eight subsections were sampled: top and bottom half; north, south, east and west quadrants. The inner circle in each pie diagram represents the upper half of the tree, and the outer circle represents the lower half. Two trees were sampled. On each sampling date, 240 fruit were examined.


NORTH
TREE 1
TREE 2
AUG 17
1 7 4 8 6 2 2 0
10 8 0 0 10 1 8 2
AUG 19
6 2 2 1 0 3 7 1
2 16 5 0 4 1 4 6
AUG 23
2 0 5 4 14 6 2 0
2 4 6 8 10 4 11 4
TREE 1
TREE 2
AUG 26
5 5 2 4 14 6 9 7
6 14 9 9 5 4 6 4
AUG 29
6 7 5 4 21 11 11 1
10 5 13 12 7 13 8 11
AUG 31
10 10 6 10 20 7 5 8
10 11 7 10 12 12 8 4

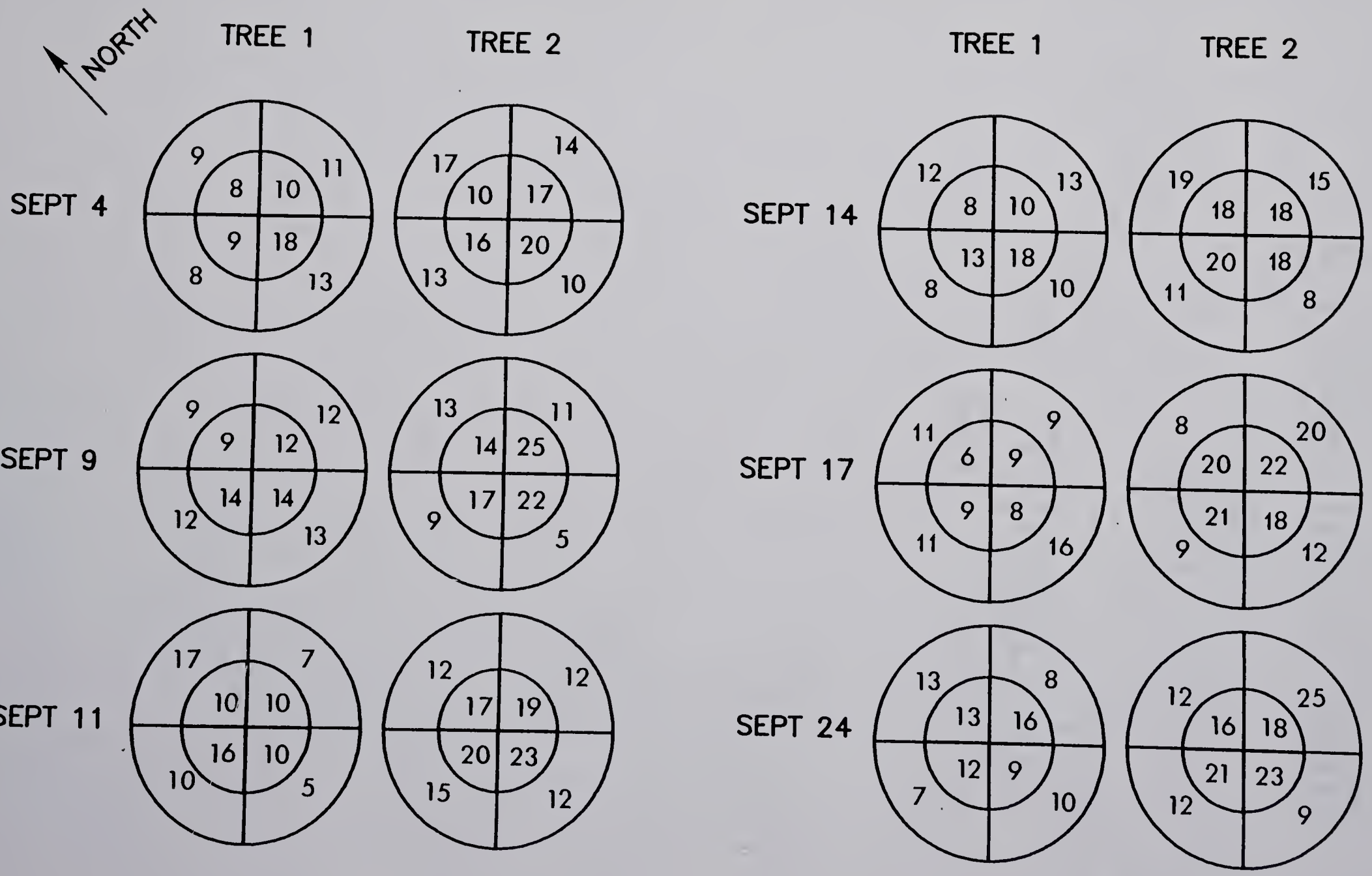

NORTH
TREE 1
TREE 2
SEPT 4
9 11 8 10 9 18 8 13
17 14 10 17 16 20 13 10
SEPT 9
9 12 9 12 14 14 12 13
13 11 14 25 17 22 9 5
SEPT 11
17 7 10 10 16 10 10 5
12 12 17 19 20 23 15 12
TREE 1
TREE 2
SEPT 14
12 13 8 10 13 18 8 10
19 15 18 18 20 18 11 8
SEPT 17
11 9 6 9 9 8 11 16
8 20 20 22 21 18 9 12
SEPT 24
13 8 13 16 12 9 7 10
12 25 16 18 21 23 12 9

Table 21. Distribution of R. pomonella eggs between trees, between levels of the tree crown, and among north, south, east, and west quadrants.

Date	Total number of eggs							
	Tree		Crown level		Quadrant			
	Tree 1	Tree 2	upper	lower	north	south	east	west
Aug 17	30a	39a	31a	38a	15a	5a	23a	26a
Aug 19	22a	38a	23a	37a	15a	11a	19a	15a
Aug 23	33a	48a	57a	24b	15a	13a	16a	37b
Aug 26	52a	57a	53a	56a	22a	21a	32a	34a
Aug 29	66a	79a	86a	59b	34a	36a	28a	47a
Aug 31	76a	74a	85a	65a	33a	31a	41a	45a
Sept 4	86a	117b	108a	95a	44a	61a	52a	46a
Sept 9	95a	116a	127a	84b	45a	54a	60a	52a
Sept 11	85a	130b	125a	90b	56a	50a	48a	61a
Sept 14	92a	127b	134a	95b	57a	54a	56a	52a
Sept 17	70a	130b	113a	93a	45a	51a	60a	50a
Sept 24	88a	136b	128a	96b	54a	51a	69a	52a

For a given date, values within the same subcategory (tree, crown level, or quadrant) followed by a different letter are significantly different at the 5% level.

Table 22. Analysis of variance of R. pomonella egg counts in fruit sampled in August and September, 1982 from 2 C. mollis trees. The trees were divided into upper and lower crown levels and north, south, east, and west quadrants. For each sample date, 240 fruit were sampled.

Source of variation	df	F					
		AUGUST					
		Date of sample					
		8/17	8/19	8/23	8/26	8/29	8/31
Main effects							
Tree (T)	1	.14	3.29	1.89	.29	1.59	.31
Level (L)	1	.64	3.86	10.48***	.17	5.82*	2.47
Aspect (A)	3	2.10	.67	3.69*	.62	1.45	1.36
Interactions							
T x L	1	5.69*	6.63**	2.80	.05	.12	.21
T x A	3	.74	1.49	.38	3.15*	4.65**	2.44
L x A	3	1.24	4.44**	.38	.44	.54	1.70
T x L x A	3	.81	3.81**	1.43	1.40	2.73*	1.57

Table 22, continued.

Source of variation	df	F					
		SEPTEMBER Date of sample					
		9/4	9/9	9/11	9/14	9/17	9/24
Main effects							
Tree (T)	1	6.10*	3.89	12.03***	13.96***	15.38***	15.88***
Level (L)	1	.42	13.50***	9.41**	9.56**	2.23	13.15***
Aspect (A)	3	1.29	1.44	1.30	.53	.60	.06
Interactions							
T x L	1	.23	2.50	3.03	16.88***	18.70***	.67
T x A	3	.67	1.22	2.85	2.47	2.53	2.19
L x A	3	2.77*	1.88	1.93	1.03	.66	2.94*
T x L x A	3	1.54	.98	.70	.65	.67	.48

* $p < .05$; ** $p < .01$; *** $p < .001$

aggregated dispersion, subsequently a random dispersion, and finally, an even dispersion. The initial aggregation of eggs may have been due to elevated female "oviposition drive" combined with subtle differences among fruit. Rhagoletis pomonella adult emergence was somewhat non-synchronous with hawthorn ripening. Thus, in mid-August when I began sampling, there were many mature females in the trees, but most fruit were hard, green, and could not be penetrated for oviposition. Perhpas when a female found a site on a fruit where she could successfully oviposit, she deposited several eggs, and thus, eggs were clustered at a single site on the fruit. Under circumstances of abundant available fruit and normal female "oviposition drive," a female rarely deposits a second egg in the same host fruit before leaving. Egg clustering could also result from different flies finding the same penetrable spots on the same fruit.

Following fruit ripening and what appears to be a transitional period where dispersion pattern was random on two sampling occasions, dispersion of R. pomonella eggs among fruit was uniform and remained uniform until fruit abscission. These results suggest an ecological significance of oviposition-deterring pheromone deposited on the fruit surface following egg-laying, because pheromone was probably the principal factor mediating the

observed uniform dispersion in September. For C. mollis fruit, irrespective of size, the amount of pheromone deposited following a single oviposition is sufficient to deter a majority of arriving females. A less critical factor, which may contribute to even spacing of eggs, is aggressive encounters between females (Biggs 1972, Boller and Prokopy 1976). Female R. pomonella have occasionally been observed to actively defend hosts against conspecifics. Further, egg dispersion may be influenced by decreased propensity of females to oviposit in fruit which contain larvae. Small fruit (9 mm diam) containing second or third instar larvae and large fruit (18 mm diam) containing third instar larvae are significantly less acceptable for oviposition than uninfested fruit (Chapter III). Of course, as cautioned by Myers and Harris (1980), this analysis of dispersion among host fruit can only suggest and cannot identify the mechanisms responsible for the dispersion.

Whatever the mechanism underlying observed dispersion patterns, most ripe fruit (ca. 75%) contained a single egg. As a result, most of the larvae should have been assured ample developmental resources and minimal intraspecific interactions. Larvae developing in singly-infested fruits realize greater survivorship and pupal weight than those in multiply-infested fruit, and

pupal weight is correlated with such important components of adult fitness as days to female maturity and oviposition rate (Chapter IV).

My finding of a uniform dispersion of R. pomonella eggs among C. mollis fruit agrees with results for a number of other tephritid fruit flies that utilize ODP's (Prokopy 1976), and is consistent with data suggesting uniformity of egg dispersion among apple fruit in Quebec (Leroux and Mukerji 1963). By contrast, my findings conflict with those of Reissig and Smith (1978), who found a random egg dispersion among Crataegus holmsiana hawthorn fruits sampled at 2 sites from mid-August to mid-September in New York.

Discrepancy between the Massachusetts and New York results could be due to greater rainfall in the latter study or sampling procedure factors (Prokopy 1981). More likely, as suggested by Reissig and Smith (1978), the New York results can be explained by observations reported by Hafliger (1953). Hafliger hypothesized, and subsequently observed, that oviposition by Rhagoletis cerasi (which deposits an ODP) follows a uniform pattern until approximately 50% of all fruit are infested. At this point, the incidence of multiple punctures is rare. When a foraging female encounters several infested fruit in succession, a change in the fly's level of discrimination

may be observed, possibly as a result of adaptation of ODP receptors on the fly's tarsi (Bowdan 1983). Regardless of the mechanism involved, females may begin to "give up" efforts to "seek out" remaining uninfested fruit and oviposit randomly. For each fly, the "giving up" threshold may be different. Ultimately, however, a random dispersion of eggs among available fruit might be realized. In the Reissig and Smith study, as a result of frequent encounter with unsuitable or infested, ODP-marked fruit, a shift in female discrimination levels could have already occurred and females could have been dispersing eggs randomly by the time Reissig and Smith began sampling. This is probable due to several factors. When the New York study was initiated, adult populations were already well established and ca. 40% of fruit sampled were infested at both sites. Additionally, it appears that the number of truly available acceptable fruit may have been substantially lower than the number apparently available (see Weins 1984): throughout the sampling period, approximately 50-70% of fruit sampled contained punctures without eggs. This suggests that although the hawthorn trees appeared laden with uninfested fruit, a female may have successfully completed oviposition only 3-5 times for every 10 oviposition attempts. I attribute this phenomenon to skin toughness and fruit hardness,

although fruit chemical factors may also have been important (Dean and Chapman 1973).

By following the entire oviposition period of R. pomonella on hawthorn, I had hoped to evaluate Hafliger's (1953) hypothesis, as described above. In my study, 50% infestation occurred near the end of August. Several days after this, fly activity began to decline. Although percentage of infested fruit continued to increase to a peak of about 70%, no shift away from a uniform egg dispersion was noted, and thus, Hafliger's hypothesis is not supported. Perhaps this was due to an exceptionally low fly population: during the course of this study, 25% percent of sampled hawthorns remained uninfested and the mean number of eggs/fruit did not exceed 1. Adults were rarely observed in trees. In comparison, in 1981, in a preliminary study of mine, no uninfested fruit were collected, the mean number of eggs per fruit was ca. 4.5 (Table 23, Site D), and adults were frequently observed. These 1981 data reflect the characteristically high infestation levels of C. mollis in western Massachusetts (personal observation). (Reductions in 1982 adult populations could have been due to near drought conditions during the summer. Some authors have suggested that low soil moisture may result in pupal desiccation and formation of a hard soil crust which hinders adult

Table 23. Preliminary 1980 and 1981 counts of R. pomonella eggs per C. mollis fruit in random samples. Trees sampled are not the same as those sampled in 1982.

		Number of eggs/fruit											
Site	Date (n)	0	1	2	3	4	5	6	7	8	$\bar{x}$	s^2	χ^2 a
A	9/15/80 (82)	6	16	41	15	3	1	0	0	0	2.0	.94	16.8 *
B	9/12/80 (51)	2	14	18	17	0	0	0	0	0	2.0	.76	15.2 *
C	9/12/80 (39)	0	10	11	14	4	0	0	0	0	2.3	.93	11.2
D	8/24/81 (82)	0	1	3	11	14	19	12	9	13	5.2	3.36	3.7
D	8/30/81 (71)	0	2	10	19	17	12	4	5	1	3.8	2.29	4.1
D	9/17/81 (75)	0	1	6	14	11	11	13	8	6	4.6	3.43	7.0

a Chi-square values in the final column were calculated by comparing the observed egg dispersion with that expected in a Poisson distribution.
Starred values indicate a significant departure from random at the 5% level.

emergence (Britton and Good 1917, Caesar and Ross 1919, Phipps and Dirks 1933)). Smaller sample sets of C. mollis fruit in 1980 at higher fly densities and moderate infestation levels ($\bar{x}$ eggs per fruit = ca. 2), I have observed both uniform and random dispersions (Table 23). Egg dispersion at Sites A and B had χ^2 values that barely approximated significance at the 5% level, and thus, did not strongly depart from random. In 1981, when fruit were heavily infested ($\bar{x}$ eggs per fruit = 4.5), I observed random R. pomonella egg dispersion among ripe hawthorns on successive sampling dates (Site D, Table 23). Thus, Hafliger's hypothesis cannot be rejected, or accepted for R. pomonella on the basis of available data. On the other hand, Remund et al. (1980) found no support for Hafliger's hypothesis for egg dispersion of R. cerasi egg among cherries: regardless of infestation level, there was a high level of uniformity of eggs among fruit.

In summary, the results of any dispersion study of individuals within a population that utilize host discrimination cues must be evaluated in light of population density and comparative quality, quantity, and distribution of suitable available resources, as well as changes that may occur in these parameters over time. Unfortunately, it may be difficult or impossible for the human observer to discern what is a "suitable available

resource" to the foraging insect (Prokopy et al. 1984). For example, at the outset of my study, when the majority (85%) of fruit was uninfested, a small number of green fruit contained multiple punctures with eggs clustered at a single site on the fruit. This suggests that differences (e.g. quality, ripeness, or skin toughness) existed not only among fruit, but also within sites on a single fruit. To my eye the fruit were homogeneous. Remarkable morphological and physiological variability may exist in a single plant (Herrara 1982, Whitham 1983, Schulz 1983, Denno and McClure 1983, Seo et al. 1982).

Distribution of eggs within and between trees

Though some differences in egg density between levels and between trees were observed following fruit ripening in September, the differences were not very great (approx. 30%). Further, a difference in egg number according to upper or lower tree level was noted in only one tree. Schulz (1983) has recently enumerated some of the factors (e.g. sunlight, wind) that may account for observations of intra- and inter-tree variation in insect abundance. Among north, south, east, and west quadrants, though, egg densities were remarkably similar. Overall, these observations are fairly consistent with earlier studies conducted on apple trees. Leroux and Mukerji

(1963) and Cameron and Morrison (1974) found no significant distributional differences among trees or crown quadrants or between crown levels for any immature stage of the apple maggot.

In conclusion, this and earlier findings of a uniform dispersion of apple maggot eggs among host fruits and within host trees are significant in providing evidence that the apple maggot fly appears to have well developed behavioral mechanisms that can lead to a remarkably high degree of both exploitation of available hosts and avoidance of intraspecific competition during larval development.

In this and other species where the immatures exploit exhaustible resource units such as fruits, buds, or seeds, it appears that oviposition-deterring pheromones are a very critical element in host selection (see references above), and that mediation by these stimuli frequently results in even dispersion of immatures among resources. As pointed out by Myers et al. (1981), in cases where oviposition-deterring pheromones have been reported for folivorous species, concomitant observations of uniform egg dispersions have not been reported, although studies of the sorghum shoot fly may provide an exception (Ogwaro 1978, Raina 1981b). Alternatively,

because folivores presumably are less likely to exhaust their resources (Hairston et al. 1960) and frequently are more vagile as larvae (and thus can emigrate from unsuitable or depleted host plants), oviposition deterrents may have a less powerful effect on egglaying folivores as compared, for example, to the deterrent effect of ODP observed in the apple maggot fly. In point of fact, Rothschild and Schoonhoven (1977) found the presence of Pieris brassicae oviposition-deterring pheromone on host plants to be only moderately inhibiting to egglaying females. They suggest that for this butterfly, the pheromone's role is simply to urge the female, fluttering among the cabbages, to "try her luck just a little further on." In this case, other qualities of the plant (e.g. age and size) or habitat are probably far more critical in ultimate host selection.

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